THE EFFECTS OF ALTITUDINAL FACTORS CONTROLLING THE GROWTH OF TROPICAL TREE SPECIES WITH PARTICULAR REFERENCE TO MALAYSIA

by

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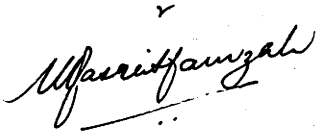
ORIGINALITY OF THESIS

Except where acknowledged the research work reported in this thesis is entirely that of the author.



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ABSTRACT

The highland forests of Peninsular Malaysia, lying between 300m–900m, comprise c.40% of the total productive forest of the country. These forests, recently included into the Forest Estate, posed new silvicultural problems centring on the development of a new silvicultural system. Basic to this are the problems associated with regeneration. Knowledge of the highland ecosystem and of the effects of environmental factors on growth, distribution and differentiation of highland vegetation is indeed relevant. It thus forms the subject of the present study which comprises a review of the literature and experimental works conducted on several tropical highland tree species.

The review of literature suggests the following:

(1) The tropical highland environment is extremely diverse with a recognised series of altitudinal vegetation zones characterised by physiognomy, flora, local climate and soil. The environmental factors controlling plant growth and distribution are unknown. The primary role of climate and secondarily of soil has been suggested.

(2) Climate is important in the control of growth of lowland species. This is supported by the relationship of growth patterns of lowland species to seasonal rythm.

(3) Intraspecies differences exist in highland vegetation especially in species with wide altitudinal range.

Introductory experimental work was conducted with the major objective of studying the growth response of seedlings of tropical

tree species to variations in day and night temperatures, light intensity, frost and moisture treatments. The species used were Pinus caribaea var. hondurensis B and G, Pinus oocarpa var. ochoterenai Schiede from Central America, Pinus kesiya Royal ex Gordon from the Philippines and Eucalyptus decaisneana from Portuguese Timor. Except for P. caribaea, a lowland species included for comparison, seed sources of all species were collected from widely spaced altitudes covering most of the species range but generally within limited latitude and longitude. The factors studied were either precisely controlled (temperature and frost) or partially controlled (light intensity and moisture). Growth analysis technique was mainly used in the interpretation of results. Results of the moisture experiment were not reported in the thesis.

It was clear from the experimental work that intraspecies differentiation occurs in tropical highland species with wide altitudinal range. Differential growth responses to variation in day and night temperatures, light intensity and frost treatment were significant. A speciation process that is adaptive and must necessarily incorporate physical environmental factors (different from the processes proposed for lowland tropical species) was suggested. The temperature experiment with P. kesiya also suggests that altitudinal variation in growth may be greater than geographical variation between disjunct seed sources of equivalent altitude.

The importance of careful sampling of seed sources of highland tropical species in provenance trials was emphasised. For this purpose the technique of growth analysis was considered useful

in view of its speed and accuracy in assessing variations in growth rate and productivity, especially in controlled experiments. Other applications of the technique included the determination of environmental conditions important to growth, for the mapping of potential distribution and location of trial sites and in the selection for improved growth rate and productivity. Caution in the field projection of results was emphasised.

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

TABLE OF CONTENTS

Page No.

INTRODUCTION

In 1963, a Land Capability Classification was conducted in Peninsular Malaysia with the aim of optimising the use of land within the framework of the Nation's development strategy. In the subsequent reclassification of land use much of the lowland forest estate was excised for higher priority uses leaving a total of approximately 10 million acres reserved for forestry. Of this, c.40% were virtually untried areas lying above the 300m contour, hitherto taken as the upper limit of the forest estate. It is clear that future expansion of forestry in Peninsular Malaysia will have to be in the highland regions. Indeed, large areas are already designated for plantation and exploitation.

The increasing attention paid to forestry in the highland areas of Peninsular Malaysia centres primarily on the problems of developing a new silvicultural system for the highland forests. Towards this end a knowledge of the ecosystem, in particular of environmental factors important in the growth, distribution and variation of timber species is essential. Accordingly it was decided to conduct a broad study into this subject.

The study outlined in the thesis comprises a review of literature (Parts I - III), a pre-experimental section (Part IV), an experimental section (Part V) and a general discussion (Part VI).

Part I of the review outlines the basis and framework of the study. The importance of forestry in the economy of Malaysia and its future role in the light of the above mentioned change in

land use was examined (Chapter 1). As a framework to the study, an outline of forests and forestry practice in the highlands of Peninsular Malaysia including a review and discussion on silvicultural problems is incorporated in Chapter 2. The ecosystem of the tropical highlands is systematically outlined in Chapter 3 with emphasis on its complexity. Factors considered important in differentiating highland vegetation are identified.

In Part II, the environmental processes controlling the growth of lowland tropical species are reviewed since surprisingly little is known of the subject with respect to tropical highland species. Growth pattern and growth phenology of tropical vegetation is examined (Chapter 4). It is clear that the majority of tropical species display a periodic pattern strongly related with seasonal rythm. The climatic control of plant growth is accordingly reviewed and important controlling factors identified (Chapter 5).

In view of the highly diverse tropical highland environment the question of genetic differentiation of tree species is important and relevant to forestry. This is accordingly reviewed in Part III with liberal examples from the temperate areas since little work has been done on this subject in the tropics.

In Part IV, the relevant findings of the review are collated and, together with information available of the experimental materials, used as guidelines in defining the scope for experimental work (Chapter 7). Materials, general facilities, experiments conducted and general methodology were then outlined in Chapter 8.

Part V comprises the experiment section of the study. The major objective for experimental work was "to conduct broad

studies on the effect of several environmental factors which vary with altitude on species with wide altitudinal ranges in the tropics". The factors studied include temperature (Chapters 9-11), frost (Chapter 12), light intensity (Chapter 13) and moisture stress. The latter experiment was not reported in the thesis.

Part VI (Chapter 14) is a general discussion of experimental findings. The importance of growth analysis technique to forestry work with reference to Peninsular Malaysia is discussed.

PART I

LITERATURE REVIEW

An Outline of the Basis and Framework of Study

CHAPTER 1

THE ROLE OF FORESTRY IN THE MALAYSIAN ECONOMY AND ITS FUTURE PROSPECTS IN THE LIGHT OF CHANGING LAND USE.

This chapter discusses the role of forestry in the national economy of Malaysia, in particular the economy of Peninsular Malaysia, and future prospects in the light of recent extensive changes in the pattern of land use and of changing demands in wood and wood products.

1.1 THE PRESENT AND FUTURE ROLE OF FORESTRY IN THE MALAYSIAN ECONOMY

As forestry is a primary industry, its importance to a national economy is generally greatest during the country's early developmental phase. In Peninsular Malaysia, the forestry sector contributed 4.37% to the Gross National Product in 1971 (valued at M$411,000,000) and directly providing employment to about 29,000 people (Ismail, 1972).

The forestry sector also figured prominently in the international trade of the country. As export items, timber and timber products ranked third after rubber and palm oil, earning M$249,500,000 in 1970. This represented an increase of two and half times over the past five years (Anon., 1974a).

Over the same period however, local consumptions of paper and paper products increased three fold to 145,118 metric tons, costing

approximately M$100,000,000 in imports. Consumption by the year 1990, is projected at 410,000 metric tons, a three fold increase from 1970 (Ismail, 1972).

It is clear that the industry will have to expand in order to meet rapidly increasing demand. Based on present trends it is estimated that approximately 200,000 acres annually will have to be reforested and rehabilitated, providing employment for about 100,000 people (Ismail, 1972).

Forestry in Malaysia is not regarded solely in terms of wood production. Indeed, the range in goods and serivces is continually expanding in the light of changing social needs from the traditional production of wood and water to such intangibles as recreation and urban beautification. Forestry is thus a permanent and versatile industry able to suffice the varying needs of the community in the various phases of economic development of the country.

The future ambitious role intended for forestry in the Malaysian economy has been outlined by Ismail (1972).

> "In the field of agro-based industries, wood will provide a healthy diversification of products. The availability of renewable raw material enhances the opportunity of expanding industrial growth to include secondary and tertiary wood processing industries. The potential for short-fibred pulp manufacture from industrial wood residues, supplemented by the more effective utilisation of the available growing stock, is good and so is the scope of plantation of long-fibred pulpwood. Short-fibred pulp for the production of various grades of paper and paper

boards is in heavy demand and this demand is steadily increasing. The world demand in newsprint is also growing and Malaysia has the potential to supply these products. Still more encouraging is the fact that while the supply of high quality tropical hardwood is diminishing, their demand is increasing. Higher financial return and more foreign exchange earnings can thus be anticipated. Forest industries will become more viable and employment, social and economic opportunities will increase".

1.2 THE CHANGING PATTERN OF LAND USE IN PENINSULAR MALAYSIA AND ITS POTENTIAL IMPACT ON THE PRACTICE OF FORESTRY

Traditionally, Malaysian society has largely been agrarian with a life style that had relatively little impact on the forested ecosystem. The scale and pattern of land use has however changed dramatically in modern times. The most profound change has been the massive clearing and reclassification of forest land for agriculture, often resulting in the excision of large tracts of prime managed Lowland Dipterocarp Forests (Section 2.2.2). In 1963 a technical sub-committee on Land Capability Classification was set up to devise an optimum national land use plan within the framework of the nation's overall development strategy (Leong, 1968).

Under the classification scheme, mining was given top priority of land use, followed by agriculture, thence forestry. These major land uses are however subject to other priority uses which include reservations for aboriginal settlement, water conservancy, game, grazing and national parks. Forestry was largely assigned to 'Class IV' lands comprising lowlands marginal to agriculture, swamps and steep-land above $18\frac{1}{2}\%$ gradient.

It is clear therefore the planned development of the Forest Estate will have to be made in the hill areas. Thus, forests lying between 300m to 1000m, hitherto protected, will be brought under production. Above 1000m, forest operation is generally thought to be uneconomic, hazardous or detrimental to the environment.

Table 1.1 shows the pattern of land use following classification for the states of Pahang, Johore, Melaka and Negri Sembilan in Peninsular Malaysia. It is clear that the major proportion of land area in all states are mainly reserved for mining and agriculture leaving an estimated total of 10 million acres of productive Forest Estate. Of this area, over 40% or approximately 4 million acres, lie above the 300m contour, the approximate upper limit of the Lowland Dipterocarp Forest. The figure however may vary between states. Thus there will be a move of a considerable proportion of the Forest Estate into a virtually untried area.

TABLE 1.1 Land Use Pattern in Selected States of Peninsular Malaysia. (Lee, 1968)

	Pahang		Johore		Melaka		N. Sembilan	
		%		%		%		%
Total State Area ('000 ac)	8,869	100	4,692	100	415	100	1,642	100
Area below 300m countour	7,057	81	4,534	97	407	98	1,343	82
Area for mining or agric.	4,412	50	3,089	66	342	82	1,033	63
Total prod.for.	2,622	30	543	12	8	2	433	26
Prod. forests above 300m	1,126	13	214	5	1	-	243	15
Prod. forests below 300m	1,496	17	329	7	7	2	190	11
Prod. for.below 300m as % of total prod. forests.	57		60		82		61	

Inconsistencies due to rounding off

1.3 THE PROSPECT OF FORESTRY IN THE HIGHLANDS OF PENINSULAR MALAYSIA

The impact of the changing pattern in land use will be felt most acutely in the indigeneous hill forests. The failure of the Malaysian Uniform System of Silviculture to satisfactorily regenerate these forests necessitates the development of an alternative silvicultural system specifically adapted to the hill areas. The Malaysian Uniform System, which aims at enriching managed stands, was mainly designed for the primary Lowland Dipterocarp Forests where regeneration is usually adequate (Burgess, 1970). Despite the lowland forests' relatively more accessible terrain, with a less complex ecosystem than the hill forests, the Malaysian Uniform System took nearly fifty years to evolve. Given the complexities of the highland environment (Chapter 3), the naturally poor regeneration of the hill forest (Section 2.3) and the utmost urgency of the whole venture, the problems that will be encountered in developing a viable hill silvicultural system has been rated "as the biggest challenge to forestry research since the evolution of the Malaysian Uniform System", (Anon., 1970).

The future prospects for plantation of exotics have already been stated. Pilot projects with P. caribaea var. hondurensis have largely proved successful (Freezaillah, 1966) and large scale plantation is currently planned for Peninsular Malaysia and Sabah (Anon., 1974b). Although in Peninsular Malaysia, plantation projects are largely confined to the Lowland Dipterocarp Forest zone the potential for planting exotics above this zone have also been tested.

The successful development of a hill silviculture system and the choice and establishment of exotics in plantation programmes will depend on an adequate understanding of the ecology of the highlands. One main line of enquiry should centre on determining the optimum growth condition of seedlings of highland species and allied with the detection of genetic variation. Such autecological studies would assist in understanding successful regeneration conditions, in determining the potential limits for productive growth, and the possible extension of a species outside of its natural distribution and in the selection of provenances for optimum matching with plantation sites.

The study outlined in this thesis is essentially introductory and primarily aimed at a broad survey of factors likely to be involved in the establishment of seedlings in the tropical highland environment and in elucidating the probable existence of genetic variation in tropical highland species.

CHAPTER 2

FORESTS AND FORESTRY IN THE HIGHLANDS OF PENINSULAR MALAYSIA

2.1 INTRODUCTION

The chapter outlines the forests and forestry in the highlands of Peninsular Malaysia as a perspective to the policy changes outlined in Chapter 1.

2.2 VEGETATION TYPES IN THE HIGHLANDS OF PENINSULAR MALAYSIA

2.2.1 Zonation of Tropical Highlands

Zonation patterns in tropical highland vegetation have been reported by various workers from various studies covering phytosociology (Brown, 1919), floristics (van Steenis, 1934) and ecology (Brown, 1919; Askew, 1964; Grubb and Whitmore, 1966). Richards (1964) in a review of some of the findings discerned an altitudinal pattern common for the wet tropics, with zones demarcated by four altitudes which he considered critical. These are 1,000m, 2,400m, 4,000m and 4,500m.

The vegetation is thus demarcated into five principal zones. Richard's (1964) terminology is adopted here except for the lower two zones in which case Grubb and Whitmore's (1966) proposal is used. The formation-types are:

1. The Lowland Rain Forest (Tropical Rain forest and Submontane Rain forest of Richards) 0 - 1,000m

2. The Montane Rain Forest 1,000 - 2,400m

   a. The Lower Montane Rain Forest

   b. The Upper Montane Rain Forest

   (Subdivisions by Grubb and Whitmore)

3. The Tropical Subalpine Forest 2,400 - 4,000m

4. The Tropical Alpine Scrub and Chomophyte formations 4,000 - 4,500m

5. Nival Chomophyte Vegetation 4,500m+

Actual zonal contours are however variable since the rate of change of climatic factors vary from place to place (van Steenis, 1934; Troll, 1958; Richards, 1964). The most common variation is due to the Mass Mountain Elevation Effect whereby zonal contours are depressed with proximity to the sea and with isolation of ridges and peaks, (van Steenis, 1961; Richards, 1964). Zones on higher mountains tend to broaden as is the case with the Montane Rain Forest zone on the main range of the Andes, in Ecuador, which ranges from c.1200-1500m to c.3200-3600m, (Grubb and Whitmore, 1966).

Some characteristics of the zones are of interest. The 1,000m altitude, the lower boundary of the Montane Rain Forest zone, is marked by a sharp increase in fog frequency with elevation (Brown, 1919). It is also the lowest altitude for permanent existence of temperate elements of the highland flora (van Steenis, 1961) which occur in abundance in the Upper Montane Rain Forest (Richards, 1964).

The 4,000m altitude, the upper boundary of the Tropical Subalpine Forest zone, is the climatic tree limit and the 4,500m altitude is the climatic snow line.

2.2.2 Vegetation Zones of the Malaysian Highlands

In Peninsular Malaysia the forest vegetation was originally classified by Symington (1943). Symington's classification was basically ecological and this was modified by Wyatt-Smith (1963), changing the emphasis to 'forest importance'. Both classifications are detailed in Appendix I.

The altitudinal distribution of Malaysian forest vegetation using Wyatt-Smith's classification within Richards' altitudinal zones is given in Figure 2.1. In this section the main vegetation zones of the Malaysian Highlands are outlined.

In Wyatt-Smith's classification the Dipterocarp forest in lowlands is altitudinally divided into three subzones: (1) Lowland Dipterocarp Forest; (2) Hill Dipterocarp Forest; (3) Upper Dipterocarp Forest. The upper two subzones, along with the Montane Oak forests (Lower Montane Rain Forest Zone) and the Montane Ericaceous forest of the Upper Montane Rain Forest Zone constitute the 'High Altitude Forests' of Malaysia. The upper two Dipterocarp subzones of the Lowland Rain Forest will collectively be termed the 'Highland Dipterocarp Subzones'.

The change in stand structure and species composition between the four forest zones and subzones of the High Altitude Forests is typical of the general altitudinal change in tropical vegetation. The latter is discussed in greater detail in Chapter 3. Figure 2.2 illustrates the typical profile and species composition of these forests. A brief outline is given below:

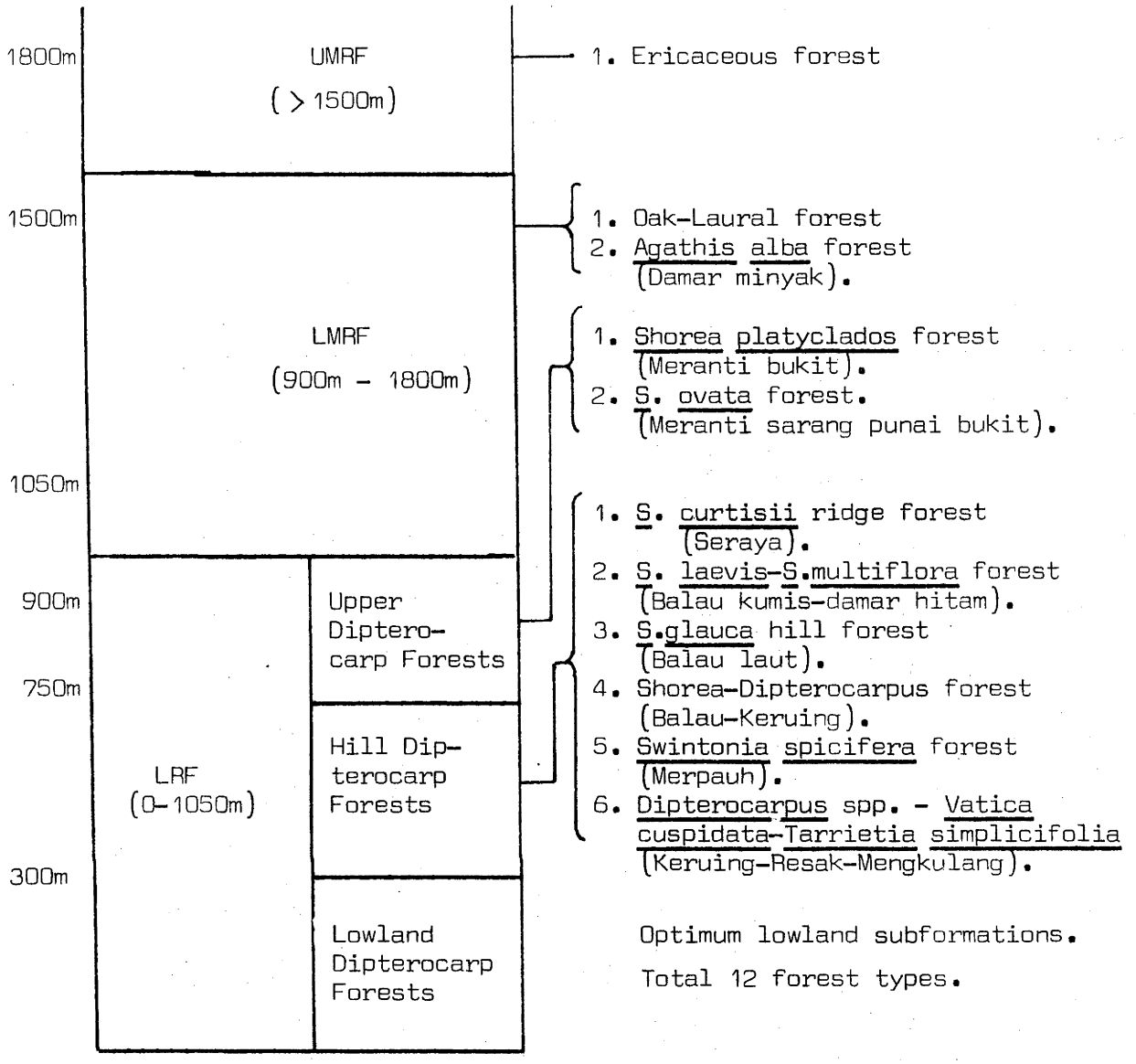


FIGURE 2.1 Altitudinal floristic zones in Peninsular Malaysia. (Robbins and Wyatt-Smith, 1964).

FIGURE 2.2 Altitudinal Forest Formation Series in Peninsular Malaysia. (Wyatt-Smith, 1963)

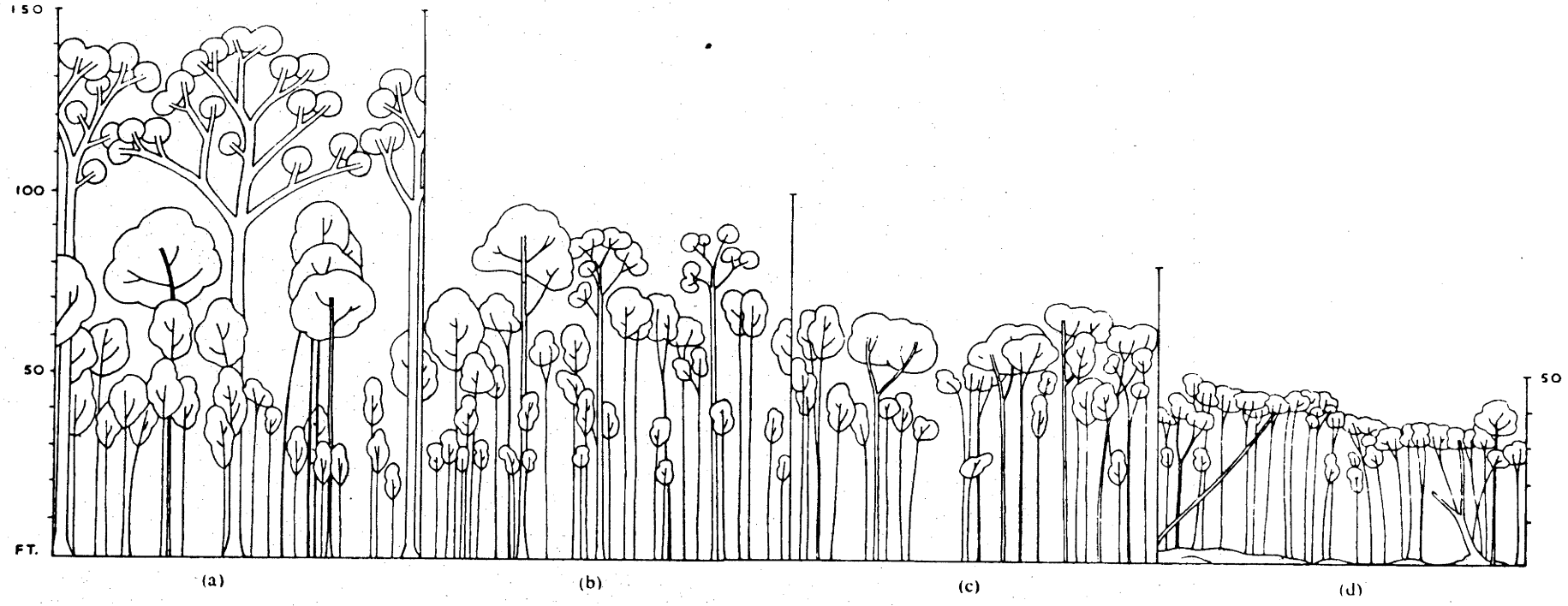
(a) Red meranti-keruing forest. 150m a.s.l. Jenka Forest Reserve, Pahang. (Lowland Rain Forest - LRF).

(b) Upper dipterocarp forest. 800m a.s.l. Kedah Peak, Kedah. (Lowland Rain Forest - LRF).

(c) Lower montane oak-laurel forest. 1500m a.s.l. Gunong Berembun, Cameron Highlands, Pahang. (Lower Montane Rain Forest - LMRF).

(d) Montane ericaceous forest. 2000m a.s.l. Gunong Berembun. Cameron Highlands, Pahang. (Upper Montane Rain Forest - UMRF).

Each section represents an actual strip of forest 100ft x 25ft. The first two sections (a and b) belong to the lowland formation (LRF). Dominated by Dipterocarpaceae (open crowns) the formation incorporates many forest types differing in stature and floristic composition but exhibits the 3-storied tree strata throughout its range from the lowland plains to the upper hill zone (Upper Dipterocarp Forest). The third section (c) shows the 2-storied tree strata of the lower montane formation (LMRF) whilst the last section (d) shows the 1-storied montane forest formation (UMRF).


150
100
50
FT.
50
(a)
(b)
(c)
(d)

(a) Hill Dipterocarp Forest (Lowland Rain Forest Zone)

The forest generally occurs between 300m and 760m altitude but in sheltered valleys the upper limit may be higher.

The transition from the Lowland Dipterocarp subzone to the Hill Dipterocarp includes a change in the composition of the dominant species, although some species exist in both zones.

There is also a marked aggregation of individuals of the same species within the Hill Dipterocarp Zone contrasting with the greater heterogeneity of the Lowland subzone. Thus the most common species on the ridges is Shorea curtisii.

Stand structure differs slightly from that of the Lowland Dipterocarp forest, varying particularly however, with topography. The stand is generally three layered. Individuals on ridge tops are comparable in size to those of the Lowland Subzone but are decidedly greater in terms of stand density. Locally, individuals on ridge tops are generally larger in size and also greater in stand density compared to those growing on slopes and valley bottoms.

(b) Upper Dipterocarp Forest (Lowland Rain Forest Zone)

The forest is generally located between 760m and 1200m altitudes. The subzone borders the upper limit of the Lowland Rain Forest and shows distinct change in flora and structure from the lower subzones.

In contrast to the Lowland and Hill Dipterocarp forests the number of species of the Dipterocarpaceae is greatly reduced. Those that do occur are distinctive and unique to the subzone. Common Dipterocarp species are Shorea platyclados, Dipterocarpus costatus,

Dipterocarpus retusus, Shorea ciliata, Shorea ovata and Shorea submontana. Common non-Dipterocarp species include Agathis alba, Calophyllum spp. and Melanorrhoea spp.

Stand structure and physiognomy differ from the preceding Hill Dipterocarp forest. The top storey of the three-storied stand is lower with a more even canopy level. The lower two stories tend to be less distinct. Individuals are smaller and incidence of buttressing less common. Density of pole-sized individuals is however, fairly similar. Litter accumulation is more noticeable.

In general the Highland Dipterocarp Subzones are characterised by the presence of distinct vegetation units. These are basically associations of dominants and co-dominants, often occupying specific topographic situations. In view of their forest importance their brief descriptions are given in Appendix II.

(c) Montane Oaks or Oak-Laurel Forests (Lower Montane Rain Forest)

This forest occurs between 1000m and 1500m average altitudes. Flora and structure differ markedly from those of the Higher Dipterocarp Subzones.

Species of the Dipterocarpaceae occur rarely; the flora is dominated by the Oak-Laurel family, i.e. the Fagaceae (Quercus, Lithocarpus, Castanopsis) and Lauraceae. Other common species include Acer niveum, Adinandra spp., Agathis alba, Calophyllum spp., Canarium spp.,Dacrydium spp., Engelhardia spp., Eugenia spp., Garcinia spp., Gordonia spp., Podocarpus spp., Santiria laevigata and Toona spp.

The stand is two storied with fairly even canopy level. Individuals are shorter, 20m-25m, and smaller. Buttressing is rare and weakly expressed. Litter accumulation is higher than that of the Highland Dipterocarp Subzones.

(d) Montane Ericaceous Forests (Upper Montane Rain Forest)

The forest occurs beyond the Montane Oak-Laurel forests and well within the belt of high fog frequency in the Upper Montane Rain Forest. The vegetation is highly distinctive of the Upper Montane Rain Forest type.

The Dipterocarpaceae is completely absent and the Oak-Laurel families drastically reduced in size. The dominant family is the Ericaceae with such species as Pieris ovalifolia, Rhododendron spp., and Vaccinium spp. Other common species are Arthrophyllum montanum, Anneslea crassipes, Buseus spp., Elaeocarpus mastersii, Eugenia spp., Garcinia spp., Ilex spp., Myrsine posteriana, Pentaphylax arborea, Phoebe declinata, Rhodamnia cinerea, Symplocos spp., Ternstroemia japonica, Teractomia tetrandra and Tristania merguensis.

Stand structure is typical of the Upper Montane Rain Forest. Trees in the stand are one-storied, averaging 10m in height, commonly gnarled and heavily covered with epiphytes. The accumulation of mounds of litter, peat and acid humus is distinctive of the forest.

2.3 SILVICULTURE IN THE MALAYSIAN HIGHLANDS

2.3.1 Silvicultural Problems

The major silvicultural problems of the highland forests, in particular the more exploited Hill Dipterocarp Forests, stem from the large number of economic species, their uneven distribution and stand density and poor regeneration. For more productive forestry and sound silvicultural management it is imperative to promote chosen economic species within relevant constraints.

The most important problem is inadequate regeneration of desirable species. According to Mok (1968) the method of solving the regeneration problem will essentially constitute the basis of a new silvicultural system for the subzones. There are several causes of poor regeneration both natural and artificial. Natural causes include infrequent and irregular flowering and weed competition, whilst the major artificial cause is damage caused by harvesting.

Flowering and fruiting of most hill species are usually irregular and infrequent (Burgess, 1969; Wyatt-Smith, 1963). The good fruiting years of Shorea and Dipterocarpus species occur at intervals of five to ten years. In addition insect damage to flowers and fruit can be considerable.

Natural regeneration is hampered by weeds. The most common and important weed is Bertam (Eugeissona triste), a stemless palm commonly and characteristically associated with Seraya ridge forests (Wyatt-Smith, 1963). It frequently forms dense thickets 5m to 7m in height, inhibiting regeneration of Seraya seedlings. The luxuriant fronds deprive the regeneration of moisture, cast heavy shade and cause mechanical obstruction to regeneration (Burgess, 1970).

Regeneration damage due to harvesting is common. Economic considerations dictate the preferential logging of ridges where the more desirable species and their regeneration are usually dense. Damage to regeneration in this situation is inevitable.

Associated with harvesting are the further problems of exposure and weeds. Wide canopy openings on ridges often lead to large scale seedling mortality through insolation and dessication (Lall,

Gill and Wan Hassan, 1968). Cockburn and Wong (1969) has demonstrated the susceptibility of Seraya seedlings to dessication in their early germination period. In addition, unrestricted throughfall during the wet season often results in rapid runoffs causing mechanical damage to seedlings (Burgess, 1970).

Environmental disturbances in addition, stimulate weed growth or promote invasion of secondary forest species. Problems due to Bertam have already been discussed. In addition, disturbed valley bottoms and slopes are often invaded by bamboos (Wyatt-Smith, 1963). These species are characteristically fast growing and easily outcompete the slower growing seedlings of economic species.

2.3.2 Possible Silvicultural Improvements in the Highland Dipterocarp Subzones

There are two major areas where silviculture can maximally contribute to the productivity of the Highland Dipterocarp Subzones. (1) Assisting regeneration; (2) Extending the distribution of economic species.

Regeneration can be assisted through enrichment planting and the control of weeds. The former necessitates a steady and reliable supply of seedlings - a difficult requirement in a situation of infrequent and erratic seeding. Lall Gill (1969) has shown that buffer stocks of 'wildings' (bare rooted seedlings collected from the forest floor) can be successfully and economically raised in local nurseries for such purposes. Moreover, the survival rate on transplanting has been shown to be quite high.

Weed control rather than eradication, especially of Bertam, is generally favoured. Complete eradication may create exposure problems (Burgess, 1969) or merely lead to a replacement by other weed species (Chong, 1970). Furthermore, Burgess (1970) has pointed out that the seedling layer is also held in check by root and light competition of upper storey trees and is not necessarily released by Bertam control alone. As a control measure, moderate slashing of fronds is recommended to allow in enough light without jeopardising the moisture regime.

The natural distribution limits of a species may be determined by factors which can be modified silviculturally. For example, Grubb (1971) suggested one of the factors controlling the lower limit of distribution is competition. Accordingly, if this hypothesis holds true for a desirable species its lower limit might be extended through the removal of competition. Lall Gill (1969) has demonstrated that seeds of Shorea platyclados transplanted well beyond its lower limit showed a high germination percentage and fast seedling growth rate. Such experiments, designed to determine potential and productive distribution limits, controlled or otherwise, are prerequisite to large scale plantings. Once these limiting parameters are determined favourable conditions can be created through site amelioration.

Site amelioration should be minimal where ecological consequence is unknown. It must be stressed that the ecology of these hill forest environments is complex. It is advisable therefore, to choose species for planting whose range can be extended with minimal site modification. Silvicultural treatment may involve removal of

uneconomic species, checking of weeds and manipulation of canopy cover. Canopy manipulation can certainly be useful in releasing seedlings from light and root competition and in speeding up mineral cycling in valley bottoms (Lall Gill and Wan Hassan, 1968). If extension can be achieved with minimal stress on the extended species and the ecosystem, maximum productivity of the Highland Dipterocarp Subzones can be realised.

CHAPTER 3

ENVIRONMENT OF THE TROPICAL HIGHLAND FOREST

3.1 INTRODUCTION

The chapter examines the tropical highland environment in a wider perspective as a background to the ensuing discussion on plant growth and distribution in Chapter 4. In particular, the chapter outlines in detail the changes with altitude in botanical and physical components of the environment with emphasis on the individualisation of altitudinal zones.

The place of tropical vegetation in general and tropical highland vegetation in particular within the context of world vegetation, is first discussed using Holdridge's classification system.

3.2 TROPICAL HIGHLAND FOREST AND WORLD VEGETATION

World vegetation has been classified by Holdridge using a bio-ecological system, (Holdridge et al., 1971). Holdridge's classification appears to have an advantage over previous systems (for example Schimper, 1898) in giving a more detailed categorisation of tropical vegetation.

Holdridge's system has three levels of classification. At the primary and basic level is the 'Life Zone' which is defined by climatic factors; mainly, biotemperature, precipitation, moisture availability and potential evaporation. Subdivisions of the life

zone on the basis of vegetation and land use constitute the secondary and tertiary levels of classification. The world environment is thus divided into over one hundred life zones arranged according to latitude of origin, altitudinal belt and humidity province (see Figure 3.1).

The tropical environment has thirty eight life zones and is characterised by high mean annual bio-temperature, total annual precipitation and potential evapo-transpiration. At the opposite climatic extreme are the Polar environment and its high altitudinal equivalent, the Nival altitudinal belt. An increase in altitude is thus characterised by lower biotemperature, precipitation and potential evaporation.

3.3 CHANGES IN BOTANICAL COMPONANT WITH ELEVATION

Stand structure, physiognomy and floristics undergo definite changes with altitude and it is possible to identify the various altitudinal zones by the combination of vegetation features considered characteristic to each zone.

Features of structure and physiognomy considered useful in characterising altitudinal zones are given in Table 3.1. These are detailed in Appendix III.

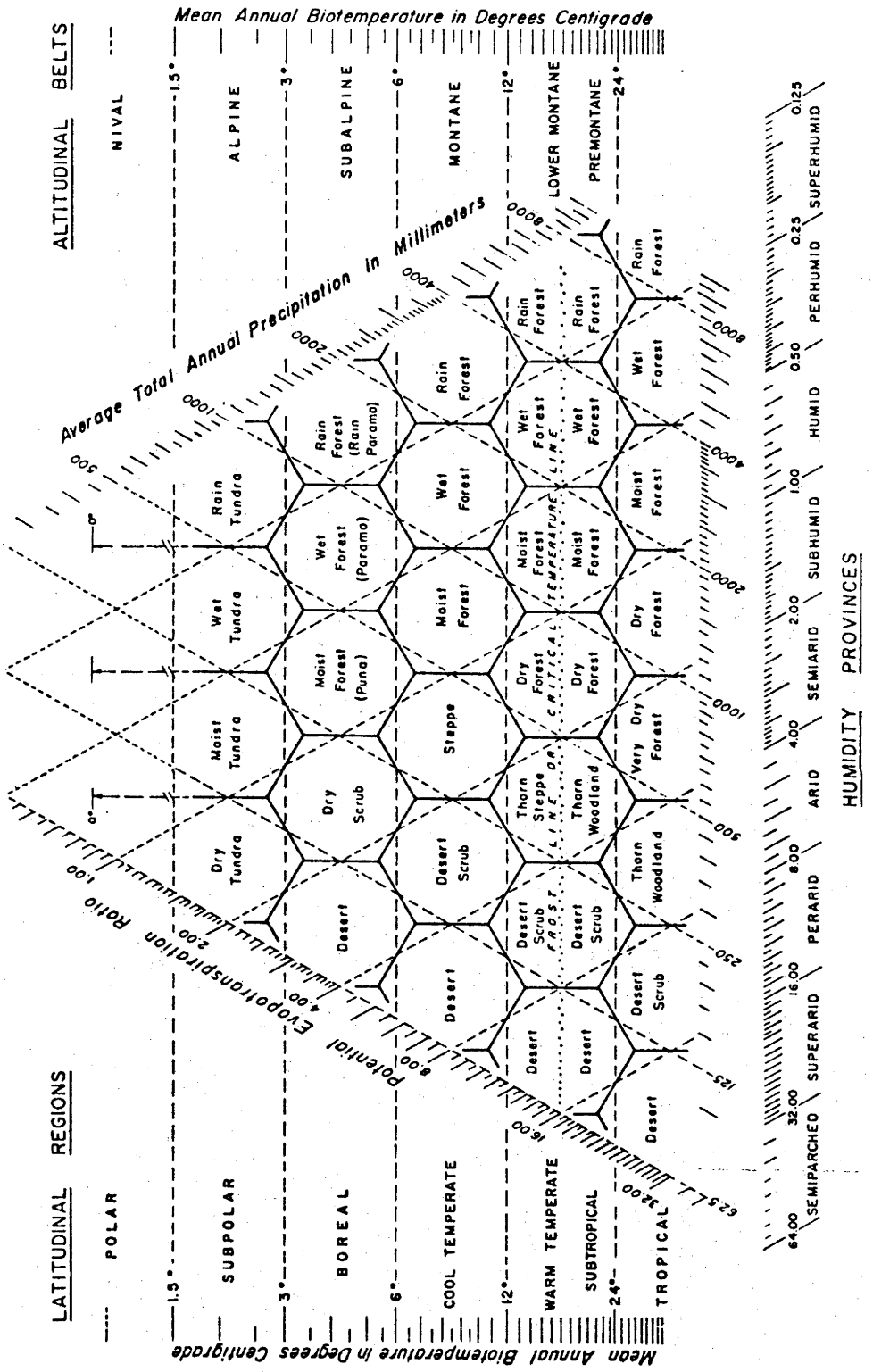


FIGURE 3.1 Diagram for the Classification of World Life Zones. (Holdridge et.al.,1971)

TABLE 3.1 Characters Considered Useful in Classifying Altitudinal Vegetation Zones in the Tropics (Grubb et al., 1963).

Leaf size predominance		LRF Mesophyll	LMRF Mesophyll	UMRF Microphyll
Climbers:				
	Photophytes	Large woody spp. common	uncommon	uncommon/ absent
	Skiophytes	common/occasional	common	uncommon
Epiphytes:				
	Vascular	common	abundant	common
	Non-vascular	common	abundant	very abundant
Others:				
	Height	24-36m(-45m)	15-27m	4.5-18m
	Tree strata No.	3	2	1
	Buttresses	usually frequent and large	uncommon or small	nil

Underlined characters are considered most important.

LRF = Lowland Rain Forest LMRF = Lower Montane Rain Forest

UMRF= Upper Montane Rain Forest

3.3.1 Stand Structure

The number of tree strata decreases with altitude. From a three storied stand in the Lowland Rain Forest it decreases to two stories in the Lower Montane Rain Forest and one storey in the Upper Montane Rain Forest. The phasing out of each stratum along zonal transitions is gradual and occurs without appreciable change in main storey height (Brown, 1919).

Zonal transitions are normally accompanied by marked changes in stand structure. Brown (1919) and Grubb et al., (1963) recorded an increase in proportion of the smaller sized trees in the Montane zones and a decrease in density of tree seedlings, but a contradictory trend in the density of herbs.

Changes in the abundance of the dependent synusia - climbers and epiphytes - are more definite and are considered by Grubb et al., (1963) to be most useful in characterising the zones. Large woody photophyte climbers are common to the Lowland Rain Forest but minimum or absent in the upper zones (Beard, 1946). Vascular epiphytes are abundant in the Lower Montane Rain Forest (Grubb et al., 1963) while non-vascular epiphytes are most abundant in the Upper Montane Rain Forest (Fulford et al., 1970). In general climbers decrease with elevation and epiphytes increase.

3.3.2 Physiognomy

There are characteristic changes in physiognomy between zones. The change in individual tree features are particularly marked. Brown (1919) recorded decreases in average tree height, diameter, tree and stand volume with altitude. Tree form deteriorates from tall clear boles in the Lowland Rain Forest to stunted gnarled crooked and low branching forms in the Upper Montane Rain Forest (Beard, 1946). Also at higher altitudes the frequency of monopodial branching decreases (Grubb et al., 1963) and the crowns of the dominant trees flatten out from the umbrella shape common in the Lowland Rain Forest (Richards, 1936). In general, the average tree deteriorates in overall size and biomass and in quality and quantity of wood with elevation.

The decrease in overall size, termed 'dwarfism', is characteristic of altitudinal change although it is also affected by topography, being more pronounced in exposed situations.

Other physiognomic changes with elevation occur in leaf characterisation and structure, cauliflory and buttressing. Changes in leaf size and shape occur with elevation. Mesophylls are generally found in all zones and form the bulk of the leaf size spectrum but macrophylls decrease in abundance especially across the Lower Montane - Upper Montane Rain Forests ecotone (Brown, 1919; Howard, 1969). Indeed an abundance of microphylls is characteristic of the Upper Montane Rain Forest (Brown, 1919). In addition, compound leaves decrease with elevation becoming negligible or entirely absent in the Upper Montane Rain Forest (Brown, 1919; Beard, 1946).

An additional important feature of leaf change is an increasing expression of xeromorphism with altitude. Leaves in the Lowland Rain Forest are generally thin and large. The epidermis is single layered and palisade cells, several layered. In the Upper Montane Rain Forest the leaves are relatively thicker and more fleshy with multi-layered epidermis and relatively fewer palisade layers (Howard, 1969).

Other aspects of xeromorphism have also been reported (Lam, 1945). As with dwarfism, xeromorphic features are accentuated by more exposed situations such as ridge tops.

Cauliflory and buttressing, characteristic of the Lowland Rain Forest, disappear at the upper limit of the Lower Montane Rain Forest (Richards, 1936). The disappearance is gradual and marked by decreasing frequency of individuals exhibiting the traits (Brown, 1919) and by the progressive decrease in the size of buttressing (Grubb et al., 1963).

3.3.3 Floristics

Each zone can be defined by its own unique assemblage of flora. A zonal flora consists essentially of species whose optimum of distribution is located within the zone (van Steenis, 1934b). However, the distribution is not necessarily confined to the zone but is commonly transzonal.

The total number of species decreases with elevation in all subdivisions of the plant kingdom (Brown, 1919; van Steenis, 1965), but relative proportions of the higher taxa vary with altitude. For example, in Java, dicotyledons are the most abundant species at sea level, monocotyledons at 1,000m and pteridophytes at 1,500m elevation (van Steenis, 1965). At high altitudes there is a progressive increase in abundance of lower plant taxa.

Zonal affinitites of some families are well known. In the Malay Peninsula the Dipterocarpaceae dominate the Lowland Rain Forestand the oak-laurel families (Lauraceae, Myrtaceae, Fagaceae), the Lower Montane Rain Forest (Robbins and Wyatt-Smith, 1964), refer Figure 2.1. The sudden prominance of temperate Holarctic and Australasian flora in the Upper Montane Rain Forest is widely reported and suggests a great degree of ecological segregation across the Lower Montane - Upper Montane Rain Forests ecotone (Brown, 1919; Symington, 1936, 1943; Richards, 1964; pp.348-9; Robbins and Wyatt-Smith, 1964).

Oligodominance - i.e. dominance by a few species - as distinct from polydominance is a feature associated with elevation. In the Dipterocarpaceae of the Malay Peninsula forest types dominated by

one or two species are increasingly apparent in the upper two subzones of the Lowland Rain Forest and in the Lower Montane Rain Forest (Robbins and Wyatt-Smith, 1964). The tendency of species to congregate in relatively homogeneous stands becomes increasingly apparent with altitude.

3.4 CHANGES IN PHYSICAL COMPONENT WITH ELEVATION

In this section various factors of the physical environment, mainly climate, soil and superimposed factors, will be discussed focusing particularly on aspects likely to be important on plant growth.

3.4.1 Climate

The major climatic factors used in the Life Zone classification of Holdridge are temperature, rainfall and atmospheric moisture status. Variations in these factors associated with altitudinal change are outlined in this section. In addition, other climatic factors, light and radiation and wind, are also discussed.

At the level of the forest stand zonal climate is further modified by stand structure. To an important degree it contributes to zonal differences in stand microclimate and influences the growth of undercanopy components especially that of seedlings.

(a) Temperature

There is a steady decrease in ambient temperature with altitude although there may be variations caused by local factors, particularly fog. Mean temperature decreases at the average of $0.5^{o}C$/+100m with a range between 0.4 - $0.7^{o}C$/+100m (Mohr, 1944; Troll, 1957).

Changes in average weekly temperature between zones at the canopy level of the dominant trees are shown in Table 3.2 from data collected by Brown (1919). The general trend with elevation is an overall decrease in average weekly maximum, minimum and thermoperiod. For example, the weekly maximum and minimum temperatures at 300m in Lowland Rain Forest are 32.4/20.0°C. and the respective figures are 28.1 and 17.3°C at 1050m in the Upper Montane Rain Forest. It should be noted that the rate of decrease with elevation is uneven. This is chiefly attributable to fog influence and is discussed below.

TABLE 3.2 Average Weekly Maximum and Minimum Temperatures in the Stand at Various Altitudes on Mt Makilling (Brown 1919). Between Oct. 1912 to Jan. 1915.

Elevation m / Temperature °C	300(LRF) Max	300(LRF) Min	450(LRF) Max	450(LRF) Min	740(LMRF) Max	740(LMRF) Min	1050(UMRF) Max	1050(UMRF) Min
Undergrowth	26.3	20.6	25.5	20.8	24.3	19.4	20.6	15.7
Second storey	27.0	21.0	26.9	21.0	-	-	-	-
Dominant tree	32.4	20.0	31.3	19.6	30.4	18.1	28.1	17.3

LRF = Lowland Rain Forest LMRF = Lower Montane Rain Forest

UMRF = Upper Montane Rain Forest

An important aspect of temperature in highland environment is the occurrance of frost at high altitudes. In his classification, Holdridge et al., (1971) recognises a critical altitude termed the 'Frost line' which represents the lowest altitude of frost occurrence. Across this line marked floristic changes occur but without changes in stand structure or physiognomy. The frost line is not at a constant

altitude as it is subject to local physiognomic variations and factors such as topography and the Mass Mountain Elevation Effect is important in this regard (Riehl, 1954; Troll, 1957).

Stand structure has a moderating influence on stand temperature. The influence is increasingly felt down a vertical gradient from the upper canopy to the ground level as apparent in Table 3.2.

Average weekly maximum temperature and thermoperiod decrease towards ground level in all zones. The change in average weekly minimum however differs between zones. In the more close canopied Lowland Rain Forest and Lower Montane Rain Forest stands the average weekly minimum in the undergrowth is slightly higher than at the upper canopy level. However, this trend is reversed in the Upper Montane Rain Forest where the stand is relatively more open.

(b) Rainfall

Maximum rainfall in tropical highlands occurs at altitudes where temperature is cold enough to cause condensation. As such rainfall distribution is generally dependant on the location of these 'condensation altitudes' on the mountain, i.e. in the middle altitudes of high mountains and near the summits of smaller ones (Richards, 1964).

Seasonal variation in rainfall appears unaffected by elevation. Brown (1919) observed that on Mt Makilling in the Philippines, seasonal range as well as the seasonal pattern in rainfall remained relatively marked and similar in all zones; thus the seasonal dry period common in some lowlands also occur in higher zones. This is discussed more fully below.

(c) Fog Influence

Climate of the tropical highlands may be markedly influenced by fog (Table 3.3). As noted earlier (Section 2.2.1) fog occurs frequently above the 1000m critical altitude and generally characterises the climate of the Montane Rain Forest. In areas with very high fog frequency, the 'fog belt', the atmosphere is perpetually saturated and light drizzles are frequent (Troll, 1957). The intensity and influence of fog is reduced at the higher altitudes and fog effects are less important in the higher vegetation zones.

TABLE 3.3 Climatic Differences Between 'Fog-Free' and 'Fog-Bound' Days in the LMRF in Ecuador at 1710m Elevation (Grubb and Whitmore, 1966)

	Fog-free Days		Fog-bound Days	
	Under-growth*	Clear-ing*	Under-growth*	Clear-ing*
No. of samplings (days)	14	14	7	7
Av. Maximum Temperature ^{o}C.	19.3	25.6	16.3	19.4
Av. Minimum Temperature	12.1	11.5	13.0	13.0
Av. Daily Range in Temperature	6.1-7.1	14.1	3.3	6.4
Av. Minimum Relative Himidity %	71	67	94	84
Av. Duration of Relative Humidity 95% (h)	16-19	13.5	23	19.5
Bright sunshine (h)	-	5.5	-	0.7
Rainfall (mm)	-	2.2	-	14.8

* Reading taken under shelter at 1m. above ground.

An important influence of fog is its modifying effect on temperature. In the fog belt temperature fluctuations are dampened and temperature range reduced (Grubb and Whitmore, 1966). On fog

free days in Lowland Montane Rain Forest clearings in Ecuador the average daily maximum and minimum are 26.5/11.5°C. On fog bound days daily maximum is reduced to 19.4°C while daily minimum is elevated to 13.0°C. Daily thermoperiod is thus reduced. Effects due to fog are a major cause for uneven temperature with elevation.

Fog therefore essentially acts as a buffer moderating fluctuations in other climatic factors and narrowing their ranges. In addition humidity is increased substantially and the duration of near saturation conditions substantially lengthened.

(d) Atmospheric Moisture Status

Humidity increases with elevation up to the fog belt and this is paralled by a depression in evaporation rate (Brown, 1919). In the fog belt humidity raches its maximum while evaporation rate becomes negligible (Brown, 1919; Troll, 1957). On very high mountains, beyond the montane zones, the fog belt tapers away into drier atmosphere, accompanied by a lowering of humidity and an increase in evaporation rate.

In seasonal climates, periods of dessication characterised by high evaporation rates, are known to occur even in the fog bound montane zones. For example, on the Andes in Ecuador, Grubb and Whitmore (1966) noted that the intensity and duration of dessication periods in the Lower Montane Rain Forest are comparable to that in the Lowland Rain Forest.

(e) Light and Radiation

Light intensity and sunshine duration generally decrease with elevation up to and including the Montane Rain Forest zones (Beard, 1946). The principal factors responsible for this trend

are the incidence of fog and cloud. Increasing fog frequency decreases light intensity, dampens the range of light intensities and generally exerts a moderating influence on the annual variation pattern of light intensity (Brown, 1919). Similarly increasing fog and cloudiness increases the proportion of diffused radiation and shortens the duration of sunshine (i.e. Table 3.3), (van Steenis, 1948; Grubb and Whitmore, 1966; Baynton, 1968).

Light intensity in the stand is further modified by stand structure - in particular the amount of canopy cover and the compactness of foliage volume. The greater amount of canopy cover in the Lowland Rain Forest and Lower Montane Rain Forest reduces light intensity to a greater degree than the more open stand of the Upper Montane Rain Forest (Grubb and Whitmore, 1966; Baynton, 1968).

In addition, the greater compactness of foliage volume in the Lower Montane Rain Forest is compared to the Lowland Rain Forest substantially reduces the amount of oblique light. The stand thus receives lesser overall light intensity and over a briefer duration around the noon hours (Grubb and Whitmore, 1966).

3.4.2 Soil

(a) Altitudinal Segregation

Edaphic segregation with altitude is widely acknowledged and there are indications of edaphic affinity with vegetation zones.

The major edaphic trend with altitude is the gradual podzolisation of soil. On Mt Kinabalu in Sabah, yellow earths are found in the Lowland Rain Forest, micropodzols and podzols in the

upper Lower Montane Rain Forest and peat soils in the wetter Upper Montane Rain Forest (Askew, 1964). In Java, Mohr (1930) also recorded a generalised transition from red earths to yellow earths and finally podzols but did not indicate the altitudes at which changes occurred.

The occurrance of podzols in well drained Upper Montane Rain Forest has been widely reported (Sensitius, 1930, 1931; Hardon, 1936; Henin, 1948; Askew, 1964). The conditions in this altitudinal zone - high rainfall, good drainage and low temperature (Corbett, 1969) - are relatively more conducive to podzolisation than in any other zones.

In some cases underlying parent materials modify edaphic trends. On Mt Kinabalu sharp changes in soil type occur on different parent materials within and between vegetation zones (Askew, 1964). This is however not apparent on the Luquillo Mountains in Puerto Rico where differences in parent materials are also recorded (Wadsworth and Bonnet, 1951).

(b) Chemical and Physical Properties

Associated with the changes in soil types are trends in chemical and physical properties. The general chemical trends with elevation are shown in Table 3.4. These are: (1) increases in overall non-living organic matter, organic carbon, nitrogen, carbon-nitrogen ratio and acidity; and (2) decreases in basicity and base elements (Brown, 1919; Friend, 1946). There is no change in absolute phosphorus content (Brown, 1919). Local topographic differences are important and differences in rates of change of soil chemicals between mountains have been recorded (Brown, 1919; Askew, 1964).

TABLE 3.4 Altitudinal Changes in Some Soil Properties
Brown 1919(1); Jenny 1948a(2); Askew 1964(3)

	LRF	LMRF	UMRF	SAF	AF	Authority
Humus %	1.06	1.71	8.06	–	–	1
Organic carbon %	–	–	–	10.50	41.62	2
	6.5	43.5	41.0(9.4)	–	–	3
Nitrogen %	0.14	0.20	0.64	–	–	1
	–	–	–	0.78	2.66	2
C:N ratio	–	–	–	13.5	15.7	2
	14.6	27.2	36.8(12.0)	–	–	3
Phosphoric anhydride %	0.106	0.104	0.112	–	–	1
Sodium (Na_2O)%	0.44	0.55	0.34	–	–	1
Potassium (K_2O)%	0.241	0.189	0.170	–	–	1
Acidity pH	3.1(5.4)	2.4	2.3(3.8)	–	–	3
	–	–	–	5.8	3.3	2
Base saturation %	3(81)	–	(1.2)	–	–	3
Texture	–	–	–	sandy loam	loamy	2

( ) on valley sides. Without brackets, on ridges.

LRF = Lowland Rain Forest
LMRF = Lower Montane Rain Forest
SAF = Tropical Subalpine Forest
UMRF = Upper Montane Rain Forest
AF = Tropical Alpine Scrub and Chomophyte formations.

The altitudinal trend in organic minerals is a direct product of slowed mineralisation rate as a consequence of the lowering in temperature. This is considered by Grubb (1971) of major ecological significance to highland vegetation. Mineralisation in the tropics is retarded below 10–15°C and optimum at 35°C (Mohr, 1930). At 25°C, the equivalent of about 1000m on Mt Kinabalu mineralisation starts to lag behind litter accumulation. Consequently from the

elevations of the Montane Rain Forest and higher there is a steady accumulation of undecomposed litter (Askew, 1964). In water logged soils, chiefly in the Upper Montane Rain Forest, mineralisation is further checked often resulting in the accumulation of peat (Wadsworth and Bonnet, 1951; Askew, 1964).

Information concerning changes in physical properties of the tropical soils with altitude is relatively lacking. Generally zones above the Lowland Rain Forest are considered better structured (Brown, 1919; Jenny, 1948; Beard 1946a; Askew, 1964; Grubb et al., 1963), but examples of water logging occur, particularly in the wetter Upper Montane Rain Forest (Askew, 1964; Lyford, 1969).

3.5 SUPERIMPOSED FACTORS IN TROPICAL HIGHLANDS

Superimposed ecological factors important in tropical highlands are mainly the related factors of fire, grazing and man. These are generally associated with the higher altitudinal areas with more seasonal climates.

The use of fire in maintaining animal pastures, in hunting and agriculture is widespread in tropical highlands. In consequence, the original broad-leaved climax vegetation which is fire sensitive, is destroyed and replaced, by fire perpetuated sub-climax vegetations. Examples of these include the Sub Alpine grasslands in Java and New Guinea (van Steenis, 1968), the pine forests of the Philippines and Vietnam (Lizardo, 1957; Kha, 1966; Kowal, 1966) and the Eucalypt forests of Timor (Turnbull, pers. comm.).

3.6 DISCUSSION

It is apparent that tropical highland vegetation is primarily differentiated by climatic factors and secondarily by edaphic factors. These effects may be modified by superimposed factors, such as fire. This view is consistent with Holdridge's (1971) observation that the stable vegetation unit is largely a product of long term climatic effect and secondarily that of other factors.

The primary role of climate needs emphasis. Climatic factors not only affect plant life directly but also indirectly through the edaphic medium, through their influence on the mineralisation cycle and their conditioning and differentiation of the soil itself in the podsolisation process. Occasionally the soil exerts as independent influence which is geologically determined.

Given this premise the integrated role of temperature, light and fog are considered vital in the ecosystem. At a secondary but important level is the temperature related retardation of the mineral cycle. Collectively and in interaction with the botanic component, these factors determine the basic niches which are segregated altitudinally and identifiable collectively as altitudinal zones. The botanic component, the assemblage of flora and characteristic structure and physiognomy, reflects this zonation.

The diversity of the highland environment no doubt places strong differential selection pressures on the taxa especially those with panzonal distribution. Fournier's work in Costa Rica (1969) has shown that large families tend to have wider altitudinal ranges. The Dipterocarpaceae in Peninsular Malaysia for example, extends up to

1000m altitude and although confined mainly to the Lowland Rain Forest zone it gives rise to several species which segregate altitudinally in the Highland Dipterocarp Subzones (Robbins and Wyatt-Smith, 1964). The tendency towards genetic differentiation in taxa with wider altitudinal ranges is probably great. This possibility is further discussed in Chapter 6.

PART II

LITERATURE REVIEW

An Outline of Patterns and Control of Growth of Tropical Lowland Species

CHAPTER 4

GROWTH PATTERNS AND GROWTH PHENOLOGY IN TROPICAL VEGETATION

4.1 INTRODUCTION

There is a great complexity of growth patterns in tropical vegetation compared to those of other regions, due perhaps, to the relatively small climatic variation in tropical areas. Despite the complexity the growth patterns have been classified on the basis of meristematic activity of the apical shoot.

The chapter outlines such a classification scheme as proposed by Koriba (1958), and discusses the phenological patterns of both vegetative and reproductive growth of the plant. The studies reviewed are mainly of lowland species.

4.2 CLASSIFICATION OF GROWTH PATTERNS IN TROPICAL VEGETATION

In the tropics vegetative growth is generally seasonal. There is a period of rest, the 'rest period', usually coincidental with the dry season if this is present, and a period of shoot activity, the 'growth period', coincident with the wet season. In non-seasonal areas along the equator the period of rest is normally absent.

Within this framework there are several different growth patterns during the period of activity. Leading shoots may grow continuously or intermittently, growing apices may be terminal or lateral and growth of the branches and leading shoots may be synchronous

or non-synchronous. Koriba (1958) has used these variations to classify tropical species into three major classes:-

(a) evergrowing species

(b) intermittently flushing species

(c) multiple flushing species

the latter two classes will be termed collectively the 'Periodic Class'. The classes have the following characteristics:

Evergrowing: Apical meristem continuously and uniformly active. Found mainly in seedlings in non-seasonal areas or in rapidly growing pioneer species.

Periodic: Apical meristem only periodically active. There is an alternation between growth and pause phases.

(a) Intermittent Flushing: The predominant class throughout the tropics especially in seasonal areas. Meristematic activities are generally synchronous between different apices such as branches and leading shoots.

(b) Multiple Flushing: Meristematic activities are generally non-synchronous between different apices. Mainly found in non-seasonal areas among mature dominants especially those subjected to environmental gradients due to the size of the trees.

As a growing apex may be either terminal or lateral, the classes detailed above are further subdivided by Koriba to give six principal types of growth pattern, namely:

1. Evergrowing terminal

2. Evergrowing lateral

3. Intermittent terminal

4. Intermittent lateral

5. Multiple terminal

6. Multiple lateral

The majority of tropical tree species belong to the periodic class. For example, in Peninsular Malaysia the proportion was estimated at about 80% (Koriba, 1958). Elsewhere particularly further from the equator the proportion is higher. The rest of the chapter will mainly concern this class.

4.3 MERISTEMATIC ACTIVITY OF THE SHOOT APEX

Histology of the shoot apex and its derivations are illustrated in Figure 4.1. Histological terms used are those of Esau (1965).

Activity of the peripheral meristem promotes radial increment and leaf initiation whilst activity of the rib meristem promotes extension growth.

Histological investigation on the activity of shoot apex of periodically growing species include studies on tea (*Camellia thea*), *Callistemon viminalis* and cacao (*Theobroma cacao*), (Bond, 1942, 1945; Purohit and Nanda, 1968; Greathouse *et al.*, 1971).

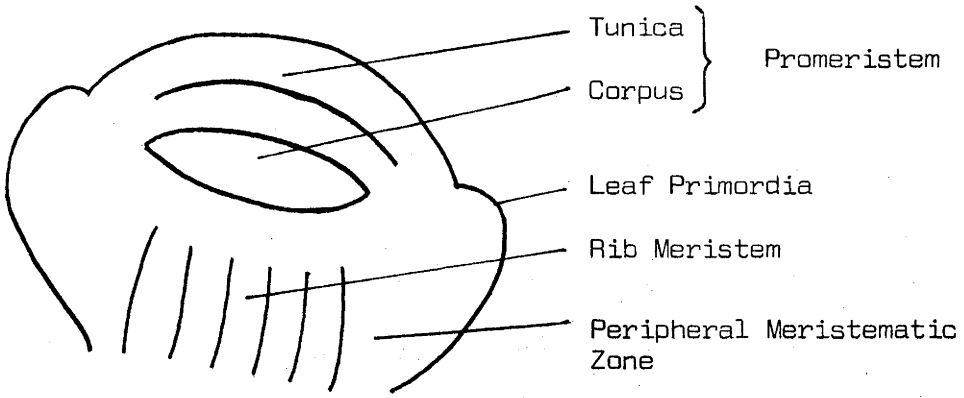
The relationships between growth pattern and meristematic activity are outlined below using examples from these studies. The periodic growth pattern has three distinct phases -

(a) the active or flush phase;

(b) the pause phase; and

(c) the rest phase.

The Shoot Apex



Derivation of Tissues and Organs

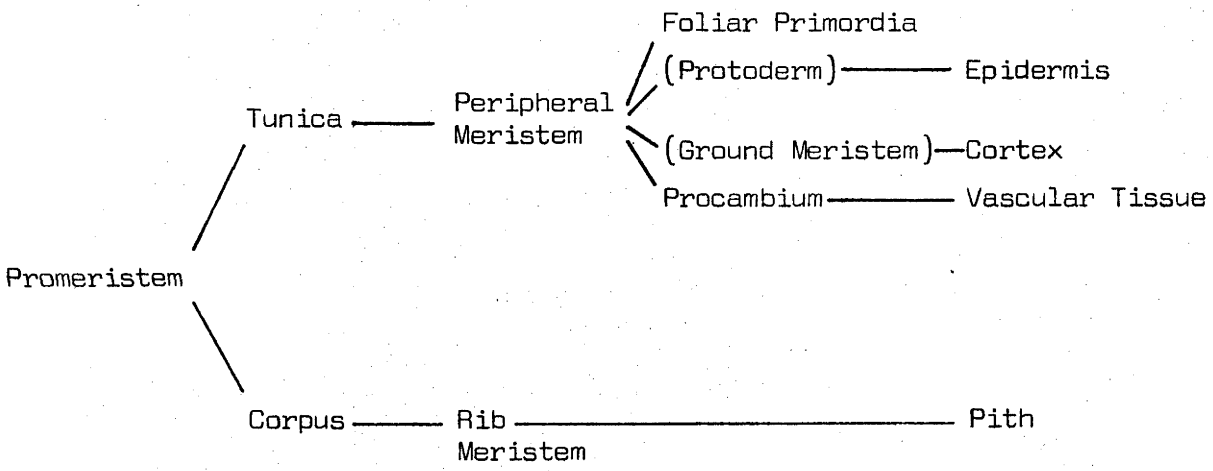


FIGURE 4.1 Histology of the Shoot Apex and Derivation of Tissues and Organs.

The flush and pause phases alternate during the growth period whilst the third phase (the rest phase) is the rest period. Species differences reported for Callistemon and cacao occur in the activity of the peripheral meristem but not of the rib meristem.

The flush phase is in general characterised by rapid extension growth as well as rapid growth of leaves. During the flush phase rib meristem is active or inactive depending on species. Thus in cacao the peripheral meristem is active, initiating new leaf primordia but in Callistemon, it is inactive, the leaf primordia having already been initiated.

Absence of extension and leaf growth generally characterises the pause phase. The rib meristem is inactive whilst the peripheral meristem may be either active or inactive. In Tea and Callistemon activity of the peripheral meristem during the phase initiates new leaf primordia and also produces radial growth.

The rest phase may or may not be similar to the pause phase depending on the species. In cacao the rest phase appears histologically a prolongation of the pause phase. However, in Callistemon the peripheral meristem reaches peak activity initiating both leaf and floral primordia and transforming the shoot into a reproductive mode.

4.4 PHENOLOGY OF THE VEGETATIVE SHOOT

The period of greatest flushing activity, the 'flushing peak', differs according to the seasonality of the area. In higher latitudes, where the climate is more seasonal, flushing peaks are also generally seasonal (Chowdhury, 1958; Hopkins, 1970; Catinot, 1970). In equatorial

areas where climate is more uniform flushing is more evenly distributed and peaks are less marked. However, in these areas peaks are often observed during the brief dry spell of the March Equinox (Holttum, 1938).

4.5 LEAF CHANGE AND ITS PHENOLOGICAL PATTERNS

The leafing habit of a tree is defined by the relationship between leaf production and leaf fall. The phenology of leaf production, as a component of shoot flushing has already been discussed (Section 4.3). Leaf fall occurs throughout the year but is however, more pronounced during the dry season (Holttum, 1931, 1938, 1940; Koriba, 1958; Ewusie, 1968; Malaisse and Malaisse-Mousset, 1970; Sharma and Rajeswaran, 1970). In general the leafing habit of tropical vegetation is complex and lacks the seasonal precision of temperate vegetation.

The leafing habit of tropical species ranges from the 'evergreen' to the 'deciduous' type. In the evergreen species leaf production and leaf fall may occur continuously throughout the year or over a limited period. In both cases leaf production overlaps leaf fall without an intervening leafless period. In deciduous species, leaf production and leaf fall occur over a more restricted period and are always separated by a leafless period which ranges from a few days to several months (Holttum, 1931, 1938; Koriba, 1958).

The various shoot growth patterns can be broadly associated with the above leafing habits. Evergrowing species are strictly evergreen, whilst periodic species, whether with intermittent or

multiple flushing pattern, may be either evergreen or deciduous. In intermittent flushing species leaf production and leaf fall are in phase within and between individuals regardless of leafing habit. In multiple flushing species however, the two processes are not in phase and leafing habits may even differ between twigs and branches of individual trees.

4.6 CAMBIAL ACTIVITY AND ITS PHENOLOGICAL PATTERNS

Cambial activity appears closely linked with activity of the apical shoot. This relationship is clear from the histological studies noted earlier (Section 4.3), and from various other studies (Chowdhury, 1961; Paliwal and Prasad, 1970; Daubenmire, 1972). Thus the periodic growth pattern tends to produce periodic cambial activity. Growth rings are therefore common in this class especially in species with deciduous leafing habits (Richards, 1964).

Although cambial activity is closely linked with the activity of the apical shoot there is often minimal overlap or an avoidance of overlap with extension growth (Chowdhury, 1958; Hopkins, 1970). The degree of overlap presumably depends on whether the peripheral meristem is active in the flush or pause phase of the growth period (Section 4.3).

4.7 VARIATIONS IN GROWTH PATTERNS

Growth patterns of the species may vary according to

(a) age and development; or

(b) seasonality of environment.

Forest seedlings that are normally evergrowing may change into periodic adults through a gradual shortening of the annual growth period (Nanda, 1963; Njoku, 1964). Thus bigger individuals in the upper stand strata show greater growth periodicity than smaller individuals in the lower strata. This gradient in growth pattern is generally recognised especially in seasonal stands (Davis and Richards, 1933; Beard, 1942; Corner, 1946).

Intra-species differences in growth pattern due to environment are also known. Distinct changes in growth pattern are known to occur between distinctly different environments as in the movement of exotic species (Holttum, 1931; Corner, 1940; Koriba, 1958) or across environmental gradients (Beard, 1942; Njoku, 1964).

4.8 REPRODUCTIVE ACTIVITY AND ITS PHENOLOGICAL PATTERNS

Four types of flowering are recognised by Koriba (1958) based on the time of anthesis. In the 'everflowering' class anthesis occurs throughout the year. In the 'seasonal flowering' class anthesis is seasonal and regular while in the 'non-seasonal flowering' class it is non-seasonal but periodic and irregular. In the 'contemporary gregarious flowering' class anthesis is irregular but occurs simultaneously in all individuals within a locality.

Species that flower seasonally are the most common even in the uniform equitorial areas where the other flowering types tend to be confined.

The time of anthesis in seasonally flowering species varies greatly from species to species although it is generally pronounced

during the dry seasons (Holttum, 1940; Richards, 1964; Ewusie, 1968; Karani, 1968). In general flowering in seasonal areas is most frequent at the beginning and end of the dry season, and minimal at the height of the dry and wet seasons (Aubreville/Richards, 1964).

4.9 DISCUSSION

Climatic variation in the tropics, although much less pronounced than in temperate areas, is still the major influence on growth phenology of tropical vegetation. This is evident from the predominance of species with vegetative and reproductive phenologies that are closely related to climatic changes, i.e. species belonging to the periodic (vegetative) class and the seasonal flowering class.

The close relationship probably suggests the importance of climate in the control of growth in tropical species as is generally known with temperate vegetation. This is further discussed in the following chapter.

CHAPTER 5

THE CONTROL OF GROWTH IN TROPICAL VEGETATION

5.1 INTRODUCTION

The chapter discusses the control of growth in tropical species. As climatic control is relatively better known and is considered important (Section 4.9), it will thus be emphasised.

5.2 CONTROL OF VEGETATIVE SHOOT GROWTH

The onset of the growth period is associated with the increase in temperature, frequency of rainfall and lengthening photoperiod while the onset of rest period is associated with the converse trends. Close relationships have been shown to exist between some of these factors and the contemporary vegetative growth phase.

5.2.1 Promotion of Growth During Wet Seasons

Although moisture is the characterising feature of seasonal change in the tropics it is not considered an important factor in controlling growth. Indeed initial flushing peaks commonly occur at the end of the dry season when moisture stress is often at its peak (Taylor, 1960; Njoku, 1963; Jeffers and Boaler, 1966; Drew, 1969; Longman, 1969; Medina et al., 1969; Catinot, 1970; Hopkins, 1970). It has been suggested that the efficient rooting systems of woody tropical species enable them to avoid surface moisture stress (Longman, 1969). However, where moisture is truly limiting it is known to exert a strong influence on growth (Alvim, 1958a; Sale, 1970a, b).

Increases in photoperiod and temperature are known to promote vegetative growth in several forest and horticultural species. For example, long days prolong growth period in several Indian forest species (Nanda, 1963), increase height and lateral growth in coffee and Terminalia superba (Alvim, 1958a; Longman, 1969) and increase the number of leaves in several West African forest species (Longman, 1966). In addition maximum temperature and daily thermoperiod promote flushings of cacao (Humphries, 1944; Alvim, 1956b and Sale, 1969).

Cambial activity may be promoted by factors associated with the climate of the wet season. Long photoperiod and high average temperature have been suggested as cambial activity controls (Alvim, 1956a; Paliwal and Prasad, 1970). However, in Dalbergia sissoo cambial activity appears to be controlled by factors of the brief dry period which normally intercede the wet seasons (Richards, 1964), i.e. low rainfall and relative humidity (Paliwal and Prasad, 1970). Thus the factors controlling cambial growth are less well known and may vary from species to species.

5.2.2 Promotion of Rest

Shortening photoperiod and decreasing temperature are considered the main factors retarding vegetative growth. Short days retard height growth, decrease lateral growth, prolong the rest period and promote leaf fall in species such as Plumeria acuminata (Alvim, 1964; Murashige, 1966; Lawton and Apkan, 1968). Decreasing night temperature further accentuates these effects (Longman, 1969).

5.2.3 Mechanisms of Climatic Control

The close correlation of growth pattern with seasonal change in tropical vegetation (Section 4.9) suggests the existence of some fundamental controlling mechanisms. Several mechanisms have been suggested based on temperature, light or their combination. The role of photoperiod alone is suspect since most experiments use unnaturally long photoperiods to produce significant results (Alvim, 1964; Longman, 1966). Its combination with night temperature is however, considered important (Longman, 1966). In addition red - infra-red (Alvim, 1964) and thermoperiod mechanisms (Alvim, 1956b; Sale, 1969) have also been suggested. However, Nanda (1963) viewed the roles of temperature and light at the more fundamental level of energy requirements of the plant. The form of energy supply, whether photo or thermic or their combination, was not important provided certain levels of requirements were satisfied.

5.2.4 Intrinsic Control of Shoot Growth

Growth patterns in some species appear innate. For example, periodic species normally growing in seasonal environments may not alter their growth patterns when grown in carefully controlled uniform environments or moved to non-seasonal areas (Koriba, 1958; Greathouse *et al.*, 1971). Stronger evidence is the tendency for grafted rubber cuttings (*Havea brasiliensis*) to conform to parental growth pattern rather than that of the stand (Schweizer/Richards, 1964). It appears that periodic growth patterns can be genetically determined and will continue to persist out of their natural seasonal rhythm even when grown in non-seasonal areas.

5.2.5 Correlation of Extension and Radial Growth

As noted earlier in Section 4.6 radial growth does not normally overlap the period of extension growth. Under favourable conditions there is an apparent competition for food and hormones between the two processes and cambial growth is generally minimised (Alvim, 1956a). This correlation and the resultant growth pattern are considered to be under hormonal control in tropical species (Chowdhury, 1958; Kozlowski and Greathouse, 1970).

5.3 CONTROL OF REPRODUCTIVE GROWTH

Generally, flowering control in the non-seasonal and everflowering species is probably innate, while seasonal and gregarious flowering species are under predominant climatic control. This section mainly discusses flowering in the latter group since little is known of innate control of reproduction in tropical species.

The various reproductive phases - floral inception, development and anthesis - appear closely related with contemporary climatic factors, as in the case of vegetative growth. However, considerable variation exists since reproductive phenology is variable between species and less precisely correlated with seasonal pattern (Richards, 1964).

Floral inception and development require the prevalence of factors associated with the dry season. For example, moisture stress and short photoperiod are considered prerequisites for floral inception (Piringer and Borthwick, 1955; Alvim, 1958a; Njoku, 1958a; Sale, 1970a). Similarly, decreasing night temperature is important to floral development due to its influence on the number of flowers (Alvim, 1958a).

Anthesis is strongly influenced by moisture availability at the end of the dry season. Adequate moisture supply and high relative humidity appear to trigger and enhance flowering (Alvim, 1960; Sale, 1970b). Alvim (1958b, 1960) suggested that the effect of moisture on flowering is hormonal. Moisture stimulates the synthesis of growth promoters which removes the influence of inhibitors imposing floral dormancy.

In gregarious flowering species of non-seasonal areas micro-climate changes are regarded more important than macroclimate changes. Actual development appears to be internally regulated but phase transitions require the prevalence of favourable microclimate cues. For example, the sudden change in moisture status and temperature accompanying a down-pour are thought to trigger gregarious flowering (Holttum, 1949).

5.4 MODIFICATION OF CLIMATIC CONTROL THROUGH VEGETATIVE AND REPRODUCTIVE INTERACTION

Climatic regulation of periodic growth may be modified by an interaction between vegetative and reproductive growth. Koriba (1958) suggested that this interaction was absent in evergreen species but present in deciduous ones.

Climatic determination of floral number and shoot phenology is modified by the vegetative-reproductive competition for food. Branches that flower and fruit profusely commonly delay flushings and leaf growth (Koriba, 1958). Cannell and Huxley (1969) and Cannell (1971) have shown that virtually all assimilates in floral branches of coffee plants (Coffea arabica) are used up in the development of fruits.

However, in cacao (Theobroma cacao)branches that produce the biggest leaf area tend to produce the most flowers (Sale, 1969).

5.5 DISCUSSION

Studies on the control of growth in tropical species are mainly confined to the role of climatic factors in regulating growth of a few important horticultural species. Indeed, not all aspects of the major climatic factors have been investigated. Despite the limitation it is apparent that climatic factors, particularly those with marked seasonal fluctuations, are the most important regulators of growth in tropical species.

Temperature and moisture are considered influential on growth. Aspects of temperature - day and night temperatures, and photoperiod - have variously been shown important to vegetative and reproductive growth. Moisture appears important mainly in reproductive growth and not in vegetative growth except under limiting conditions.

Seasonal variation in photoperiod is considered too small to be influential on the growth of tropical plants. However, its interaction with night temperature may be important and needs further investigation as does the role of other aspects of light such as intensity and quality.

PART III

LITERATURE REVIEW

Genecology of Tree Species

CHAPTER 6

GENECOLOGY OF TREE SPECIES

6.1 INTRODUCTION

In Section 3.6 it is suggested that species with a wide altitudinal range will exhibit some genetic differentiation due presumably to the differential selection pressures of the segmented highland environment. In this chapter this altitudinal variation will be examined in the context of genecology, i.e. the study of intra-species variation of plants in relation to the environment and genetics of the species (Turesson, 1923).

6.2 EXISTENCE OF INTRASPECIES GENETIC DIFFERENTIATION IN TEMPERATE TREE SPECIES

Intraspecies differences have been detected in numerous diverse characters of temperate tree species. These included leaf form in Pinus taeda and Betula alleghaniensis (Knauf and Bilan, 1974), floral structure in Pinus sylvestris (Karrafatt and Gerhold, 1973), wood properties in Populus deltoides (Posey, 1969), growth and growth phenology in Pseudotsuga menziesii (Rudloff, 1972, 1973), leaf chlorophyll in Acer negundo (Winstead and Toman, 1972) and isoenzymes in Pseudostuga menziesii (Muhs, 1974).

Evidence on the occurrence of altitudinal ecotypes in temperate tree species with wide altitudinal ranges has also been established. A study on Pinus ponderosa, a species native to the east

coast of the U.S.A. was especially well documented. Seeds were collected from open pollinated parent trees along a W-E transect on the Sierra Nevada at steps of 300m spanning a total 2100m elevation within narrow latitudes. The resulting seedlings were grown in reciprocal transplant plots within the original transect at three elevations, 288m, 820m, and 1695m. Growth was analysed at 12 years (Mirov et al., 1952), 20 years (Callaham and Liddicoet, 1961) and 29 years (Conkle, 1973). Differences in growth trend were significant in each case and related to altitudes of seed parents. Similar differences in wood properties were also recorded (Echols and Conkle, 1971; Echols, 1972).

Other studies have also reported significant differences between altitudinal ecotypes. Variations in features such as height in Pseudotsuga menziesii (Hermann and Lavender, 1968), leaf form in Abies balsamea (Myers and Bormann, 1963) and seed size in Pseudotsuga menziesii (Sweet, 1965) were considered genetically based.

6.3 ALTITUDINAL ECOTYPES IN TROPICAL TREE SPECIES

The occurrence of altitudinal ecotypes in tropical tree species is little known and the examples given by Burley and Burrows (1972) and Corn and Hiesey (1973) are probably among the first of its kind.

Burley and Burrows (1972) detected differences in needle characters among provenances of Pinus kesiya, a species with a wide altitudinal distribution and native to the island of Luzon in the Philippines (refer Appendix IV). Seedlings grown from seeds collected from two disjunct population centres, one at low altitudes

(Zambales province) and another at high altitudes (Mountain province) were compared on twelve morphological and anatomical characters of needles using multivariate analysis. The authors found significant differences between low altitude sources (Zambales province) and five seed lots of the high altitude sources (Mountain province).

Corn and Hiesey's (1973) work on Metrosidero polymorpha complex showed genetic differences which were attributed to steep environmental gradients. The taxon, a common native tree in Hawaii, is polymorphic with ill-defined taxonomic boundaries. It occurs from sea level to 2550m altitude in a broad continuous distribution over a wide variety of sites, but chiefly on wetter slopes, varying in form from tree to shrub depending on situation. Seeds collected from different altitudes were grown together at sea level in Honolulu. Variation in height and leaf form showed strong evidence of ecotypic differentiation along altitudinal gradients although variation may overlap from site to site. Seedlings from other islands compared under similar conditions also showed parallel variation patterns. Steep environmental gradients especially that of temperature and rainfall were considered important in causing the ecotypic differences.

6.4 ADAPTATION OF ECOTYPES TO LOCAL ENVIRONMENTAL FACTORS

Intraspecies variation in temperate species has been considered an adaptation to local environmental factors. In lowland species various factors have been suggested. These include climatic factors; temperature and photoperiod (Vaartja, 1959), moisture (Heiner and Lavender, 1972; Schultz and Gatherum, 1971) edaphic factors (Autonovics et.al., 1971; Jahromi, 1972) and biotic factors (Wells and Switzer, 1971; Palzer and Rockel, 1973).

In temperate highland species differences in ecotype response to frost, temperature, light and moisture have also been suggested. The frost free period is shorter at higher elevation and is widely considered the primary factor controlling the variation in growth pehnology of temperate species with wide altitudinal range. The decrease in the span of growing season (i.e. the period between bud burst and bud set) with elevation (Nienstaed and Olson, 1961; Hermann and Lavender, 1968) is considered an adaptation to avoid frost injury. Similarly, the seeds of the higher ecotypes require a longer chilling period, and hence germinate later thereby avoiding the late season frosts (Sweet, 1965; Farmer et al., 1972). Exceptions where an altitudinal trend in seed germination is not apparent, have also been reported (Mirov et al., 1952; Critchfield, 1957).

Investigations into factors regulating growth phenology of temperate highland species suggest the important role of photoperiod. Studies by Heide (1974) on seedlings of Piciea abies have shown that the critical photoperiod for dormancy is longer with high elevation ecotypes; i.e. growth dormancy is earlier at higher altitudes.

Ecotypes of higher elevations appear to have efficient energy relations in a widely fluctuating environment (Daubenmeir, 1954; Wright, 1971). For example Wright (1971) has shown higher altitude ecotypes of Pinus attenuata utilise energy more efficiently than lower ecotypes under conditions of wide temperature changes and especially under extremes of temperature. Similarly, higher ecotypes of several woody species, such as Mimulus cardinalis and Oryxia digyna utilise photoenergy more efficiently than lower ecotypes under higher light

intensities (Milner and Hiesey, 1964). Higher ecotypes appear physiologically better buffered to sudden and extreme climatic changes. A response, suggested by Wright (1971), to be critical in the upper limits of distribution.

Genetic differences in moisture relations are less well known. A field experiment by Zobel (1974) on Abies grandis suggests that altitudinal ecotypes differ in their response to moisture stress. Stomatal closure in lower ecotypes was more rapid than in higher ecotypes.

6.5 EVOLUTION IN TROPICAL TREE SPECIES

6.5.1 Reproductive System of Tropical Tree Species

Inbreeding is the predominant reproductive mode in tropical trees (Aubraville / Richards, 1964) and is promoted by the isolation mechanisms peculiar to the region (Federov, 1966; Baker, 1959) namely: (1) isolation due to low individual representation per species per area; (2) reproductive isolation due to synchronous flowering pattern particularly among non-seasonal species in the more uniform areas (Section 4.8); and (3) probable reproductive isolation through the satiation of insect and animal pollinators due to the masiveness of individual tree size and profusion of blooms.

In general the evolutionary trend is towards reproductive isolation and homozygosity with the potential for rapid genetic isolation and speciation. This is in contrast to the outcrossing, and parmixis, hence lesser speciation potential, of temperate trees (Stebbins, 1958; Baker, 1959).

6.5.2 Evolutionary Processes Proposed

The evolutionary process leading to the development of the complex tropical flora is presently unknown. It is generally conceded a long geological period of regional stability and uninterrupted rapid speciation have contributed to this complexity. Opinions differ as to the actual mechanism particularly in the relative importance of natural selection and genetic drift.

Dobzhansky (1950) emphasised the role of natural selection. He considered the equable physical environment to be relatively unimportant and emphasised the role of the botanical environment. The species form stable relationships with other competing and symbiotic species through the evolution of differential adaptive characters via natural selection. The creation of numerous niches thus resulted from and contributed to the botanical wealth of the tropical environment.

Dobzhansky's proposal appears to contradict one basic characteristic of tropical vegetation. The traditional speciation process is necessarily preceded by some form of reproductive isolation, to counter genetic continuity. Hence, closely related taxa do not generally occur close together. But the co-occurrence of closely related taxa is common in tropical vegetation (Richards, 1964).

A counter proposal forwarded by Federov (1966) is the view that genetic drift and not natural selection is the main evolutionary force in tropical environment. Essential to the argument are the contributary roles of biotic and reproductive isolation and inbreeding which promote genetic discontinuity (Section 6.5.1). Under this condition, and given the long stability in the region, mutant genes

rapidly accumulate, leading to speciation within relatively confined areas. Thus, in Federov's view, taxonomic characters of tropical species are not necessarily adaptive. Co-occurrence of closely related species is considered possible since competition is thought to exist mainly at the genus and family levels (Federov, 1966; Baker, 1959).

The roles of natural selection and genetic drift may well be more complementary than exclusive. As suggested by Baker (1969), natural selection is vital in ensuring a high degree of fitness to cope with the rigorous though generally similar demands on regeneration, characteristic of the tropical environment (Richards, 1964). The fitness adaptation may be perpetuated by the propensity towards reproductive isolation. Further speciation through genetic drift presumably operates within this framework.

The hypothesis of Rehfeld and Lester (1968) regarding the evolutionary status of species, lends credence to the speciation process discussed above. According to the hypothesis, successionally advanced species inhabiting stable and mature environments, as in climax vegetation, tends toward genetic fitness as against genetic flexibility. The breeding system is thus typically apomictic leading to fragmentisation of the gene pool.

6.6 DISCUSSION

The occurrence of intraspecies differences in temperate tree species is well established. Forest tree species with wide altitudinal ranges commonly show intraspecies differences that are

associated with altitude. Such differences are likely to exist in the complex tropical highland environment where uniqueness of zonal flora is probably the result of local adaptation (Section 3.3.3). Species with transzonal distribution are however common (van Steenis, 1934b) and may be prone to intraspecies differences due to strong differential selection pressures between zones as noted in Section 6.3. It is possible that genetic differentiation in tropical highland species is mainly an adaptive process rather than a non-adaptive one as proposed by Federov (1966) for tropical lowland species (Section 6.5.2).

PART IV

AN OUTLINE OF THE GENERAL APPROACH TO THE EXPERIMENTAL WORK

CHAPTER 7

SCOPE OF EXPERIMENTAL WORK

7.1 INTRODUCTION

The chapter reiterates and defines silvicultural problems as discussed in Chapter 2 and as associated with policy changes outlined in Chapter 1. These are examined briefly within the context of the general literature (Parts I, II,III) and information available on the species material (Appendix IV). The scope of the experimental work is then discussed.

7.2 DEFINITION OF PROBLEMS

The major silvicultural problems in Malaysian forests above 300m have been reviewed in Chapter 2. Desirable species frequently fail to regenerate in economically desirable numbers due to inadequate flowering and fruiting, vegetative competition or harvesting damage. Improvement may be effected by labour intensive operations such as enrichment planting, weeding and intensive silvicultural manipulation of the stands.

Thus planting is likely to become increasingly common in the highland forests. All the silvicultural operations required are labour intensive and approximate to full scale plantation silviculture. Indeed plantation silviculture is now being considered for some highland forests. It is therefore increasingly important to match planted material to the local environment. Yet variation patterns in tropical

vegetation, particularly highland vegetation, are relatively unknown. Studies of such variations and the factors controlling them are necessary and prerequisite to the selection of seed sources for optimum matching of planting materials to the local environment.

7.3 ESTABLISHMENT OF SEEDLINGS

A large number of environmental factors may affect growth of tropical highland vegetation as outlined in Chapter 3.

Factors considered important in regulating the growth of tropical species are listed below. Asterisks distinguish factors specifically important to highland vegetation.

List of Factors Important to Growth of Tropical Vegetation

A. Climate

1.	Temperature*	Day temperature
		Night temperature
		Thermoperiod
2.	Frost*	
3.	Light	Photoperiod
		Red - Infrared
		Light intensity*
4.	Moisture*	Moisture availability
5.	Integrated Factors*	Photoperiod x Night temperature
		Temperature x Light intensity
		Fog and associated factors

B. Soil

Nutrients*

C. Biotic Factors*

Fire

Micro-organisms

Grazing

Plant competition

7.4 SCOPE OF EXPERIMENT

The relationship between intra-species variation and environmental factors can be studied using controlled environments since factors selected for study can be regulated and general tropical conditions approximated in controlled or semi-controlled experiments. This is facilitated by the use of seedlings as experimental materials.

Accordingly it was decided to conduct broad studies on the effect of several environmental factors which vary with altitude on species with wide altitudinal range in the tropics.

As a guide to the experimental work the following criteria were followed as closely as possible.

7.4.1 Choice of Experimental Materials

Experimental material should, ideally, originate from sources which might show evidence of wide environmental differences attributable to altitude and not to other factors of situation, such as latitude or longitude.

The requirements were largely met in the seed sources of three tropical tree species. The species origin and altitudinal range were:

(a) Eucalyptus decaisneana; Portugese Timor,
500m to 2680m.

(b) Pinus oocarpa; Central America,
300m to 2400m.

(c) Pinus kesiya; the Philippines,
450m to 2450m.

(Full details of the origin of the material used are given in Appendix IV).

7.4.2 Choice of Environmental Factors

As studies on the growth of tropical highland species are generally lacking the present study was basically introductory. As many major factors as practicable were therefore studied.

The effects of four major environmental factors on growth of experimental materials were studied; temperature, frost, light and moisture.

CHAPTER 8

MATERIALS, FACILITIES, EXPERIMENTS AND GENERAL METHODOLOGY

8.1 INTRODUCTION

This chapter outlines the materials, facilities, experiments conducted and general methodology of the experimental work detailed in Section V of the thesis.

8.2 MATERIALS

Details of seed sources of the three species used and background notes are given in Table 8.1 and Appendix IV. Seed sources of E. decaisneana and P. kesiya were bulked seeds collected from several trees. Information on each seed tree was recorded (Turnbull, pers. comm.). Seed source of P. oocarpa (POM) from British Honduras was a bulk collection from the entire range of the species on Mt Pine Ridge. The range is however restricted and the sampling is considered fairly representative (Hudson, pers. comm.). No information was however available on the collection of the remaining seed sources (PC, POL and POT).

For convenience, seed sources common to a region are collectively termed a 'series'; i.e. 'Eucalyptus series', 'Oocarpa series' and 'Kesiya series'.

The Kesiya and Eucalyptus series closely met the requirements of the criteria outlined in Section 7.4.1. The former consists of two latitudinally disjunct populations, the

TABLE 8.1 Data of Origin of Seed Sources Used in Experiments

Series	Provenance*	Locality	Lat.	Longt.	Altd.
A. Eucalyptus Series		Portuguese Timor			
	EL	Dili	8°39'S	125°27'E	570m
	EM	Aifefu, Maubisse	8°54'S	125°36'E	1554m
	ET	Mt Fatamailau	8°55'S	125°30'E	2743m
B. Oocarpa Series		Central America			
	PC	Nicaragua	14°20'N	83°20'W	160m
	POL	El Cayo, Br. Honduras	17°00'N	88°55'W	380m
	POM	Br. Honduras	17°00'N	88°55'W	1000–1300m
	POT	Michoacana, Mexico	19°09'N	101°58'W	1770m
C. Kesiya Series		The Philippines			
Zambales subseries	PKSL	Cato Mine, Zambales	15°32'N	120°07'E	600–750m
	PKST	" " "	"	"	900–1100m
Cordillera subseries	PKNL	Mt Data, Bontoc Prov.	16°55'N	120°55'E	1440–1500m
	PKNM	" "	16°54'N	120°53'E	1900m
	PKNT	" "	16°52'N	120°55'E	2100m

(*) Code for provenance (seed source)

Species: E = Eucalyptus decaisneana
PO = Pinus oocarpa
PC = Pinus caribaea
PK = Pinus kesiya

Source elevation (relative)
L = Lower elevation
M = Middle elevation
T = Upper or Top elevation

Additional code for P. kesiya
N = Cordillera distribution (Northern)
S = Zambales distribution (Southern)

Cordillera and Zambales subseries, which differ latitudinally by about $1^{o}22'$. The Eucalyptus series originated entirely from Portuguese Timor. Seeds of both species were collected from well spaced altitudes which span most of their altitudinal range but were confined within narrow margins of latitudes and longitudes.

The criteria was less easily met in the Oocarpa series for the following reasons:

(1) The inclusion of a lowland seed source of Pinus caribaea var. hondurensis extended the range of the series southwards by $3^{o}20'$ (Table 8.1). The inclusion was considered necessary to complement the altitudinal range of the series since P. oocarpa does not occur below 300m altitude (Hudson pers. comm.).

(2) The series was further extended by $13^{o}3'$ west and $2^{o}9'$ north (Table 8.1) by the inclusion of a disjunct oocarpa provenance, POT. Although the seed sources, POL and POM, perfectly met the criteria they were however not available at the same time for inclusion in any one experiment. POT was thus used in both experiments (Chapter 10) partly due to its availability and also due to its high altitude of occurrence. The seed sources in the series were in general well spaced altitudinally (Table 8.1).

8.3 FACILITIES

Facilities for controlled experiments were available at CERES phytotron in Canberra. These are detailed in Morse and Evans (1962).

In the present study the major facilities used included open glasshouses, growth cabinets and frost room. The latter facility will be described in Section 12.2 together with the frost experiment.

Glasshouse facilities were used in temperature experiment with the Kesiya series and light experiment with the Eucalyptus series (refer following Section 8.4). In these glasshouses temperature and photoperiod were precisely controlled. Day and night temperature regimes were alternated in a square wave pattern with day temperature held at one level for eight hours (0830 to 1630 hrs) and night temperature held at a level $5^{o}C$ lower for the remaining sixteen hours. Relative humidity was always kept higher than 40%.

The glasshouses made maximum use of natural photoperiod through its northerly orientation. The photoperiod was extended to sixteen hours by an additional eight hours of low intensity incadescent lighting with an illumination of about 25fc. at plant height.

Temperature experiments of Eucalyptus and Oocarpa series (Section 8.4) were conducted in naturally lit growth cabinets (type 'C') situated in the glasshouses. Selected day and night temperatures were also alternated in a square wave pattern and over the same time period as in the glasshouses. Temperature was controlled precisely within $\pm$ $0.25^{o}C$ error. An atuomatic shutter device regulated natural photoperiod to eight hours (0800 to 1600 hrs). This was extended to sixteen hours by low incadescent

lighting in the cabinets with the same illumination level as in the glasshouses (25fc. at plant height). A similar humidity level was also maintained.

8.4 EXPERIMENTS CONDUCTED

A total of eight experiments were conducted using four species and twelve seed sources. These can be grouped under the four major environmental factors studied as outlined below. With the exception of moisture experiments, all experiments were conducted at CERES phytotron. The moisture experiment was conducted in the Forestry Department of the A.N.U. Details of the experiments conducted are summarised in Table 8.2.

A. Temperature Experiments

The experiments basically aimed at studying growth response of seedlings from different altitudes under different day and night temperature combinations. Seedlings of all series were used. The experiments can be subdivided according to experimental designs used, into the followings:

1. Eucalyptus - Oocarpa Series

Both the Eucalyptus and Oocarpa series were treated together under common experimental designs (Table 8.2). In one experiment, growth response of seedlings under a high day and night temperature range (24/18^{o}to 30/24^{o}C) was studied. Upon preliminary analysis of the results it was decided to complement the study with a second experiment aimed at studying growth response under limiting temperature conditions (i.e. 24/21^{o} to 15/10^{o}C). The experiments were:-

TABLE 8.2 Details of Experiments Conducted

Experiments	Age[a]	Duration of Treatment	Provenance[b]	Treatment
A. Temperature 1. Euc.–Ooc.series (a) High temp.range Euc. Series Ooc. Series	 26 days 31 days	 54 days 101 days	 EL, EM, ET PC, POM, POT	Day x Night temperature (°C) (24,27,30°C) day x (18, 21,24°C) night. 9 combinations
(b) Low temp.range Euc. Series Ooc. Series	 26 days 31 days	 54 days 162 days	 EL, EM, ET POL, POT	Day/Night Temperature (°C) (1) 15/10; (2) 18/10; (3) 18/15; (4) 18/18; (5) 21/10; (6) 21/15; (7) 21/18; (8) 24/18; (9) 24/21.
2. Kesiya Series	30 days	84 days	PKNL, PKNM, PKNT, PKSL, PKST	Day/Night Temperature (°C) (1) 15/10; (2) 15/16; (3) 15/22; (4) 21/10; (5) 21/16; (6) 21/22; (7) 21/28; (8) 27/10; (9) 27/16; (10) 27/22; (11) 27/28.
B. Frost Euc. Series	16–21wks	–	EL, EM, ET	Temp. (°C)/Duration (hrs) (1) –1/12; (2) –1/6; (3) –1/6
C. Light Euc. Series	30 days	42 days		% Full daylight intensity (1) 100% (Control); (2) 62%; (3) 51%; (4) 16%.
D. Moisture Kesiya (Cordillera) Series	5 wks.	33 wks.	PKNL, PKNM, PKNT	(1) Control; (2) Half draught; (3) Full draught

[a] Age at beginning of treatment.

[b] Code for provenance as for Table 8.1.

(a) High Temperature Range Experiment

The effects of all combinations (9) of three day (24^{o}, 27^{o} and 30^{o}C) and three night temperatures (18^{o}, 21^{o} and 24^{o}C) on three altitudes of seed sources of both series were examined.

(b) Low Temperature Range Experiment

The effects of nine combinations of four day (15^{o}, 18^{o}, 21^{o} and 24^{o}C) and four night temperatures (10^{o}, 15^{o}, 18^{o} and 21^{o}C) on three altitudes of seed sources of the Eucalyptus series and two of the Oocarpa series were examined. Two temperature combinations ($24/18^{o}$ and $24/21^{o}$C) were common with the high temperature experiment to maintain continuity.

2. Kesiya Series

The effects of eleven combinations of three day (15^{o}, 21^{o} and 27^{o}C) and four night temperatures (10^{o}, 16^{o}, 22^{o} and 28^{o}C) on five altitudes of seed sources (three from Cordillera and two from Zambales subseries)were examined

The study of temperature effects was emphasised owing to the importance of temperature in the highlands environment. In all, five temperature experiments were conducted, two each on the Eucalyptus and Oocarpa series (high and low temperature range) and one on the Kesiya series.

B. Frost Experiment

The effects of three frost treatments (-1^{o}C/12hrs and -1^{o}C/6hrs, twice) on three altitudes of seed sources of the Eucalyptus series were studied.

C. Light Experiment

The effects of four shade treatments on three altitudes of seed sources of the Eucalyptus series were studied. The shade treatments, measured in terms of relative light intensities (taking full daylight as 100%) were, 100% (control), 62%, 51% and 16%.

D. Moisture Experiment

The effects of three moisture treatments (control, 'half draught' and 'full draught') on three altitudes of seed sources of the Kesiya (Cordillera) series were studied.

A similar study was attempted on the Eucalyptus series but later abandoned owing to repeated mortality of the seedlings.

Due to insufficient time left to complete the thesis, it was not possible to include the results of all experiments conducted as outlined above. Consequently, results of the moisture experiment were not included in the thesis. No further reference will be made of this experiment.

8.5 GENERAL PLANT PARAMETERS

Parameters common to most experiments are discussed below while those specific to some experiments are discussed in the relevant sections.

(a) Stem Height: defined as the distance along the stem, between cotyledon and the first visible petiole base in eucalypts and the approximated apex in pines. In pines some subjectivity was unavoidable due to tight bunching

of apical needles around the apex, thus requiring minimum handling to avoid damage. Accuracy was ±1mm for eucalypts and ±3mm for pines.

(b) Stem Diameter: measured at the hypocotyl end approximately 2mm below the cotyledon, but avoiding any local irregularities. For consistency in periodic measurements, the spot was inked. Diameter was taken as the average of two readings (measured with a verneer caliper) mutually at right angles with each other and with the stem. Accuracy was ± 0.1mm.

(c) Branch Number and Length: a branch was defined as any lateral growth with axis $\geqslant$ 5mm. A single branch length was taken as the distance from branch base to branch apex (as defined for stem apex) and the cumulative length of all branches constituted the branch length for the plant. Accuracy was ± 1mm for eucalypts, ± 3mm for pines.

(d) Leaf Area: eucalyptus leaves were measured on a photoelectric basis with an 'Automatic Area Meter' (Type AAM-5, Hayashi Denko Co Ltd, Tokyo). Leaves to be measured were mounted flat on a continuous transparent belt. Accuracy was ± 0.01sq cm. Error may arise from overlapping of lamina, repeated measurements of leaves adhering onto belt and dirty or worn out belt. Wrinkled leaves were cut and spaced out and belt washed whenever necessary or replaced. Accuracy was checked periodically with measured standards.

(e) Leaf Dimensions: leaf length in eucalypts was defined as the distance from the first trace of lamina near the petiole to leaf tip and leaf breadth was the widest distance between two points on laminar margin at right angles to the mid-rib.

(f) Leaf Number: In eucalypts, all leaves $\geq$ 5mm length with unfolded lamina were enumerated.

(g) Dry Weight: plant parts - leaves/needles, branches, stem and root (the plant portion below cotyledon) were oven dried (fan circulated air at c.85^{o}C) for a minimum of forty-eight hours. Larger woody parts required longer periods. Materials were cooled in dessicators to room temperature before weighing. Accuracy was $\pm$ 0.0001g. To avoid moisture imbibition, especially with large surface materials - leaves and roots - exposure time between dessicator and weighing was minimised. Accuracy was checked periodically by zeroing the scale reading.

(h) Shoot Root Ratio: the ratio of shoot to root dry weight is commonly used to measure dry matter distribution within plants (for example, Ledig and Perry, 1965). The ratio is considered sensitive to variation in environmental factors and is therefore suitable in assessing the effects of these factors on plant growth (Kozlowski, 1971).

(i) Growth Analysis Parameters:

1. Mean Relative Growth Rate and Net Assimilation Rate: Mean Relative Growth Rate is a measure of productivity

and defined as the rate of increase in plant dry weight per unit time, Mean Net Assimilation Rate is a measure of photosynthetic efficiency and is defined as the rate of increase in plant dry weight (photosynthate) per unit photosynthetic tissue per unit time. The parameters are therefore functions of plant size and are considered constant over a given period (Radford, 1967).

2. Mean Leaf Area Ratio: defined as the ratio of the assimilatory material per unit of plant material present. Together with net assimilation rate it forms a component of relative growth rate. Leaf area ratio is in turn made up of two components - (3) and (4) below.

3. Specific Leaf Area: defined as the area of photosynthetic tissue per unit leaf weight. It also serves as an indicator of leaf thickness and leaf plasticity.

4. Leaf Weight Ratio: the ratio of leaf dry weight to total plant dry weight.

The determinations of these parameters are given in Section 8.7.1.

8.6 EXPERIMENTAL DESIGNS

The major objective of experimental work was to examine the possibility of interaction between selected factors and altitudes of seed source on the growth of experimental material. A factorial design was thus most appropriate and accordingly used in all experiments. The designs of individual experiments are given in Table 8.3 and details of factors and levels in Table 8.2.

TABLE 8.3 Designs and Analyses of Experiments

Experiment	Factorial Design	Analysis Conducted
A. TEMPERATURE 1. Euc.-Ooc. Series (a) High temp. range Euc. Series Ooc. Series	3 Provs. x 3 day x 3 night temps. (without replicates)	ANOVA II
(b) Low temp. range Euc. Series	3 Provs. x 9 Temps. (with replicates)	1. ANOVA II 2. Multiple Regression Analysis
Ooc. Series	2 Provs. x 9 Temps. (with replicates)	
2. Kesiya Series	5 Provs. x 11 Temps. (with replicates)	1. ANOVA II 2. Multiple Regression Analysis
B. FROST Euc. Series	3 Provs. x 4 Treatments (with replicates)	ANOVA II
C. LIGHT Euc. Series	3 Provs. x 3 Treatments (with replicates)	ANOVA II

In designing an experiment the choice of treatment levels closely approximated as far as possible natural conditions of seed sources. Exceptions were made when factors considered important were given extra levels. For example, in design of the kesiya temperature experiment, night temperature was emphasised even though this resulted in negative thermoperiods.

For simplicity of analysis only symmetrical designs were used. In some temperature experiments however, such a design was not possible at a three-factor level (provenance, day and night temperature). This was due either to inclusion of treatments considered important in the natural environment or the loss of some treatments during experiment. To achieve symmetry the day and night combination was treated as a single factor thus reducing the number of factors to two (provenance x temperature). Such a balanced two-factorial design was used in temperature experiments with the Eucalyptus-Oocarpa series (Sections 9.2 and 10.2 respectively) and the Kesiya series (Section 11.2).

8.7 CALCULATIONS AND ANALYSIS

8.7.1 Calculations

(a) Growth Analysis

Mean Relative Growth Rate (RGR) and Mean Net Assimilation Rate (NAR) were calculated as measures of growth for all harvested plants in all experiments, except for the frost experiment. The formulae given by Radford (1967) were used.

$$RGR = \frac{LnW_2 - LnW_1}{T_2 - T_1} \quad \ldots\ldots\ldots \quad (1)$$

$$NAR = \frac{W_2 - W_1}{A_2 - A_1} \times \frac{LnA_2 - LnA_1}{T_2 - T_1} \quad \ldots\ldots \quad (2)$$

Where W_1, A_1 and W_2, A_2 are respectively plant dry weight and total leaf area at the beginning (T_1) and end (T_2) of treatment. LnW_1, LnW_2, LnA_1 and LnA_2 are the natural log transformations of the various values.

In Pinus species, where the surface area of needles is difficult to measure accurately needle dry weight (L) was used in place of leaf area in determining NAR. Thus,

$$NAR = \frac{W_2 - W_1}{L_2 - L_1} \times \frac{LnL_2 - LnL_1}{T_2 - T_1} \quad \ldots\ldots \quad (3)$$

The constancy of RGR and NAR rests on the assumption of linearity in the following relationships:

Equation (1) LnW vs T

Equation (2) W vs A

LnA vs T

Equation (3) W vs L

LnW vs T

These relationships can be tested by simple regression technique for all experiments with periodic harvests. In general correlations were high ($r > 0.8$) in all experiments thus justifying both the use of the above formulae and the technique of periodic harvests.

Such tests have been emphasised by Radford (1967). Much confusion stems precisely from faulty assumptions made of complex physiological relationships, as above, in deriving growth analysis equations.

The remaining growth analysis parameters, Mean Leaf Area Ratio (LAR), Specific Leaf Area (SLA) and Leaf Weight Ratio (LWR), were calculated according to the following formulae (Radford, 1967):

$$LAR = \frac{1}{2}\left[\frac{A_1}{W_1} + \frac{A_2}{W_2}\right]$$

where W_1, A_1 and W_2, A_2 are respectively plant dry weight and total leaf area at the beginning and termination of experiment.

$$SLA = \frac{A}{W_L}$$

where A and W_L are respectively total leaf area and total leaf dry weight at the time of harvest.

Since accurate assessment of surface area is required in determining both LAR and SLA, as with NAR, these parameters were not used in experiments using Pinus spp.

$$LWR : \frac{W_L}{W}$$

W_L and W are respectively total dry weight of leaves and plant dry weight at the time of harvest. LWR is also expressed as a percentage.

(b) Transformation of Data

All percentage data were transformed into their arcsin values for analysis.

8.7.2 Analysis

Methods of analysis of the various experiments are listed in Table 8.3.

(a) Analysis of Variance

Analysis of Variance (Model II) for balanced factorial designs (Snedecor and Cochran, 1967, Chap. 12) was used in the analysis of parameters of final harvest plants in all experiments. Growth analysis parameters, RGR and NAR, of intermediate harvest plants were analysed together with those of final harvest plants.

(b) Multiple Regression Analysis

In the design of some temperature experiments,day and night temperature combination was treated as a single factor (temperature) to achieve symmetry of design (Section 8.6). The relative effects of day and night temperatures can still be measured by using the method of Multiple Regression Analysis. The independent variables, day (T_1) and night (T_2) temperatures were regressed against a given parameter (Y), the dependent variable, according to the linear model;

$$Y = a + b_1T_1 + b_2T_2$$

where 'b_1' and 'b_2' are the 'Partial Regression Coefficients' of 'Y' on 'T_1' and 'T_2' respectively and 'a' is the 'Regression Constant'.

The relative importance of T_1 and T_2 can be measured by ranking their 'Standard Partial Regression Coefficients' (SPRC) since both variables were mutually independent (Snedecor and Cochran, 1967, p.398).

$$SPRC = bi \sqrt{\sum t_i^2 / \sum y^2}$$

where t_i^2 and y^2 are the sums of squares of temperature (T_i) and total (Y) respectively.

(c) Comparison of Mean Values

Means were compared using the standard Least Significant Difference procedures. However, with a larger number of means the indiscriminate use of L.S.D. had been cautioned (Snedecor and Cochran, 1967). Duncan's Multiple Range Analysis method was used instead.

8.8 GENERAL EXPERIMENTAL PROCEDURES

8.8.1 Seed Storage and Fumigation

Whenever seeds were not in use they were stored in opaque air-tight containers in cold temperatures. Seeds were fumigated with Methyl Bromide on entry into CERES.

8.8.2 Establishment of Seedlings

Based on a germination trial and on initial temperature experiments, a procedure for the establishment of experimental materials was standardised and followed in all subsequent experiments conducted at CERES (See Table 8.4).

TABLE 8.4 Establishment Schedule for *E. decaisneana*, *P. oocarpa* and *P. caribaea* Seedlings[a]

	Schedule (day)	
	E. decaisneana	P. oocarpa P. caribaea
1. Sowing	0	0
2. Germination[b] period	4–14	9–15
3. Peak germination[c]	± 7	± 11
4. Transplant	22–23	18–19
5. End of establishment period	30	25

a. Under 27/22°C day and night temperatures with 8 hours natural and 8 hours artificial light.

b. Period with ⩾ 90% germination count. Germination criteria were, 1. eucalypts; cotyledon separated and spread, 2. pines; hypocotyl erect.

c. Average for all provenances and species. Differences between provenance on germination period and germination peak were observed in *E. decaisneana* and *P. oocarpa* especially in the former. All provenances showed bimodal pattern with a more prominant initial peak.

In the subsequent schedules from sowing to transplant the following features were common:

1. Watering Regime: Watering was twice daily but regulated according to weather conditions and stage of germination. During periods of high insolation and at early stages of germination and establishment additional watering was necessary.

2. Medium: During establishment and subsequent treatment periods a common medium (1 perlite:1vermiculite by volume) was used.

(a) Soaking

Seeds were soaked in water for about 24 hours.

(b) Sowing

Shallow germination trays or large pots with adequate drainage holes were used. Soaked seeds were sprinkled evenly on the surface of the medium, lightly covered and then sprayed with water.

(c) Germination

Seeds were germinated in the CERES glasshouse under the following conditions: $27^{o}/22^{o}C$ temperature, 8 hours natural and 8 hours artificial photoperiod and high humidity (R.H. $>$ 40%). Nutrient solution was applied once daily, at two weeks following germination and precautions were taken to prevent nutrient burns.

(d) Transplant

Seedlings selected for transplant were graded visually, aided by approximate measurements. Those with similar height, length and quantity of needles (for pines) or similar leaf pair stage, leaf shape and size (for eucalypts) were selected. To

ease pressure on roots during pricking the medium was immersed in water. Overlong roots were pruned to prevent balling. Pots of similar size and with the same sized drainage holes were used. Two seedlings were planted per pot where possible and the medium compacted to ensure good root-medium contact. Dead seedlings were immediately replaced. In general, mortality was negligible. Towards the end of the establishment period seedlings were thinned to one per pot. At the end of the establishment period seedlings were ready for treatment.

8.8.3 Grading of Seedlings for Experiments

A standard grading procedure was adopted for all experiments. For a given seed source the procedure was as follows:

1. The number of blocks, B (which equals the number of replicates per unit of experiment) and the total number of replicates for the experiment (N) were first determined.

2. Seedlings were then ranked by height. Those with abnormal features or extreme heights were removed leaving N seedlings including replicates for initial harvest (usually multiples of B).

3. Remaining seedlings were then grouped into B height classes or blocks.

4. Within each block, seedlings were randomised and alloted to treatments and initial harvests. Thus at the start of each treatment there were B replicates per unit of experiment and nB replicates for initial harvest. The latter number was adjusted according to total availability of suitable seedlings.

5. Within each unit of experiment seedlings were again randomised and allotted to harvest schedules. This step does not however, apply to the frost experiment.

8.8.4 Some Routine Procedure

The following procedures were routinely conducted in most experiments.

1. Watering and Nutrient Regimes: At CERES all established seedlings were watered twice daily 12.00 hrs and 15.30 hrs and nutrients applied once daily at 08.30hrs. The formula of the nutrient used at CERES (modified Hoagland) is given in Appendix V.

2. Pest Control: Seedlings were routinely checked for signs of fungus and insect attacks. Attacks by red spiders on Eucalyptus leaves (temperature experiment, high temperature range/ CERES) were checked with methyl bromide fumigation. Damage was in general negligible. Pest control measures were routinely conducted at CERES. In general, seedlings were free of pest damage.

3. Position Effect: Minimised through weekly randomisation of pot position.

4. Restriction of Root Growth: Seedlings considered pot bound were transferred to larger pots.

8.8.5 Harvests

Periodic harvests were made in all experiments except in the frost experiment. This technique has the main advantage of greatly reducing the workload which would otherwise be

concentrated in the final harvest thus enabling the maximum use of available space. In addition, it permitted comparison of growth analysis parameters - Relative Growth Rate and Net Assimilation Rate - since these are quite independent of age in seedlings.

PART V

EXPERIMENTAL WORK

CHAPTER 9

THE EFFECTS OF DAY AND NIGHT TEMPERATURES ON THE GROWTH OF EUCALYPTUS DECAISNEANA SEEDLINGS

9.1 INTRODUCTION

Eucalyptus decaisneana occurs over a wide range of altitudes in Portuguese Timor from 500m to over 2,600m elevation (Appendix IV). Over this altitudinal range the difference in average air temperature is estimated at 10.5°C using the universal temperature lapse rate of 0.5°C/100m (see Section 3.4.1).

There is also a wide annual variation in temperature within the species range characteristic of a monsoonal climate experienced in the region. At Maubisse (1,432m) for example, within the vicinity of the middle altitude seed source, EM, (Table 8.1) the average daily maximum temperature during the warmest month is 30.0°C and the average daily minimum temperature of the coldest month is 11.9%. The latter temperature drops further with elevation to 8.6°C at 1860m in Hato Builico. At this rate of decrease, the average minimum temperature of the coldest month at the upper limit of distribution is conservatively estimated at less than 5°C and is probably as low as 2°C.

The species is thus conditioned to a wide range of temperature due both to wide altitudinal differences and wide seasonal fluctuation. Such magnitude of differences undoubtedly impose a very strong differential influence on the growth and development of seedlings within the species.

Seed sources used in the experiment, the low (EL), middle (EM) and top (ET) altitude provenances were collected at elevations that practically span the total altitudinal range of the species. More importantly, they were collected along a continuum within very narrow limits of latitude and longitude (Table 8.1). The species is therefore ideal in the study of the effects of environmental factors related to altitude on seedling growth and development.

The object of this experiment is to study the growth response of E. decaisneana seedlings to a wide range of day and night temperature combination; in particular, to examine whether any differences in growth response occur that can be ascribed to wide differences of altitude of seed sources used.

9.2 MATERIALS AND METHODS

The experiments were conducted at CERES phytotron using seed materials supplied by the Forest Research Institute in Canberra (Seed lot numbers S10135, S10136, S9016).

Three altitudinal seed sources of E. decaisneana were used; mainly, the low altitude provenance (EL) from 570m, the middle altitude provenance (EM) from 1554m and the top altitude provenance (ET) from 2743 m elevation. Details of the origin of seed sources were given in Section 8.2 and summarized in Table 8.2.

The study comprised two experiments (Section 8.4, Table 8.2). In Experiment I, nine combinations of three day (24, 27 and 30^{o}C) and three night (18, 21 and 24^{o}C) temperatures were used. Preliminary analysis of results suggest the range to be

optimum for the growth of all three provenances. The range was consequently lowered in Experiment II which aimed at investigating possible provenance differences under limiting temperature conditions. Nine day and night temperature combinations were then used; 15/10, 18/10, 18/15, 18/18, 21/10, 21/15, 21/18, 24/18 and 24/21^{o}C with the last two regimes common to both experiments, for continuity.

The temperature regimes selected were based on actual as well as projected meterological data available of the seed source (Appendix IV). The day and night temperatures thus used were presumably within the natural range experienced by the species.

The experimental design used vary between experiments. In Experiment I a balanced three-factorial design (provenance x day x night temperature) was used. Although thermoperiods as large as 12^{o}C may not occur within the species' natural range they were however used to preserve the symmetry of design.

In Experiment II, a three-factorial design was not possible since the inclusion of certain temperature regimes considered important was given a greater priority. A balanced two-factorial design (provenance x temperature) was thus used (cf. Section 8.6).

All temperature treatments were carried out in 'C' cabinets under growth conditions and procedures outlined in Sections 8.3 and 8.8.4.

In both experiments the harvest schedule and average age of seedlings were similar (Table 9.1). Twenty-six-day-old seedlings were used following standardised establishment and grading procedures (Section 8.8.2 and 8.8.3). The treatment lasted 54 days, terminating on 11/2/71 in Experiment I and 28/8/74 in Experiment II.

TABLE 9.1 Harvesting Schedule: Temperature Experiment with Eucalyptus Series

Harvest Schedule	Age (days) since Germn.	Age (days) since Tmt.	No. of Replicates[a]	Total No. of Repl. Harv.
I/II[b]	I/II	I/II	I/II	I/II
-/1	52	26	0/1	0/24
-/2	59	33	0/1	0/24
1/3	66	40	1	27/24
2/4	73	47	1	27/24
3/5	80	54	1-3/3	54/72

[a] Per provenance and per treatment

[b] Experiment I/Experiment II

For each experiment, nine seedlings per provenance were harvested at the beginning of treatment. One seedling per provenance and treatment was harvested in harvests one and two of Experiment I and harvests one to four in Experiment II (Table 9.1). The number of seedlings per provenance and treatment in the final harvest was between one and three in Experiment I and three in Experiment II. The variation in Experiment I was primarily due to insufficient number of suitable seedlings available. The total number of treated seedlings harvested in Experiment I and II were respectively 108 and 168.

At each harvest the following primary parameters were measured: stem height and diameter, leaf area and the component oven dry weights of leaves, branches, stems and roots. In addition, branch number and length was measured and total plant weight, mean relative growth rate and net assimilation rate were calculated. In the final harvest branch number and length was also measured and shoot:root ratio, mean leaf area ratio and leaf weight ratio (as % leaf weight) were calculated. Measurement and calculation procedures were as outlined in Sections 8.5 and 8.7.

Analysis of variance (Type II) were conducted on both primary and derived data. In the analysis of mean relative growth rate and net assimilation rate, the averages of the final harvest data were used thus giving a total of three replicates per provenance and treatment in Experiment I and five in Experiment II. That gave a total of 81 replicates in Experiment I. Owing to the loss of treatment 18/15°C in Experiment II the total number of replicates were reduced to 120. The remaining analyses were conducted only on final harvest data.

In Experiment I, only average values were used for analysis thus giving a total of 27 plants. Analysis of variance was conducted as for a balanced 3 x 3 x 3 factorial design without replicate (Table 8.3).

In Experiment II, a full complement of seedling was maintained in each treatment through the use of spare plants. This allowed three replicates per provenance and treatment or a total of 72 plants. Analysis of variance as for a 3 x 8 factorial design (with replication) was conducted. In addition, a multiple regression analysis (Section 8.7.2c) was conducted to evaluate the relative effects of day and night temperature on dry-matter production.

9.3 RESULTS

9.3.1 Differences Between Experiments in Growth Response of Seedlings Grown Under Common Temperatures

Growth response of seedlings grown under common temperature regimes, i.e. 24/18°C and 24/21°C, were compared between the two

experiments to determine whether their results can be integrated. The comparison is shown in Table 9.2 below.

TABLE 9.2 Comparison of Selected Parameters of Eucalyptus decaisneana Seedlings Grown Under Common Temperatures in High (Experiment I) and Low (Experiment II) Temperature Range Experiments

Parameter		24/18°C		24/21°C	
		EXPT. I	EXPT. II	EXPT. I	EXPT. II
1. Dry-matter Production (g)	ET[a]	2.678	1.3808	2.179	0.7453
	EM	4.648	0.5959	5.673	0.9927
	EL	7.816	2.1754	6.962	1.5114
2. Stem Height (cm)	ET	25.1	13.4	21.3	8.6
	EM	51.8	13.1	61.3	18.0
	EL	22.5	20.8	54.3	14.7

[a] EL (Low), EM (Middle) and ET (High) altitude provenance.

It is clear from Table 9.2 that despite similar experimental procedures there were differences in growth response between the two experiments. For example, at 24/18°C dry-matter production in seedlings of the low provenance (EL) was three and half times greater in Experiment I than in Experiment II (respectively, 7.816 and 2.175g). Similarly, height growth in the middle provenance (EM) was greater by four times (51.8 as against 13.1cm).

Opposing trends were also apparent. For example, the different night temperatures, 18 and 21°C, increased the height growth in the low provenance (EL) seedlings in Experiment I (22.5 to 54.3cm) but decreased that in Experiment II (20.8 to 14.7cm).

Since large differences in productivity occurred, a variation in energy supply other than thermo-energy was probably involved. It was notable that Experiment I coincided with the period of the southern solar solstice, a period of maximum insolation at the latitude of Canberra (the average daily radiation level during January at CERES phytotron was c.610 g.cal/sq cm/day) and Experiment II with the northern solar solstice, a period of minimum insolation (c.280 g.cal/sq cm/day in July). It was thus probable that differences between the two experiments were due to variation in the supply of photo-energy in the open glasshouses. This however needs further investigation.

The results of both experiments will be presented and discussed together to maintain continuity. It should however be emphasised here that the interpretation and integration of their results are generally considered tentative.

Results of both experiments are given in Table 9.3 and the more important parameters shown in Figures 9.2 and 9.3. Results of analysis of variance are summarized in Table 9.4 . Means compared with Duncan's multiple range test are given in Figure 9.1.

9.3.2 Provenance Differences

(a) Growth and Productivity

E. decaisneana exhibited a clear altitudinal trend of decreasing growth and producitivity with elevation. The trend was clear in dry-matter production and growth rate (Figures 9.2a, b; 9.3a,b) but less so in stem height growth (Figures 9.2c, 9.3c). It was also more marked in the higher (Experiment I) than in the lower temperatures (Experiment II).

TABLE 9.3 Growth Response in Seedlings of *E. decaisneana* From Three Altitudes Grown Under Two Ranges of Day x Night Temperatures: High Temperature Range in Experiment I and Low Temperature Range in Experiment II.

1. Means of all parameters were calculated from final harvest data of 80 day old seedlings following 54 days under treatment. Exceptions were calculations of mean RGR and NAR (refer Methods).

TABLE 9.3 (Cont'd)

A : EXPERIMENT I – High Temperature Range

Parameters		Day Temperature °C			Night Temperature °C			Prov. Av.	LSD[a] (5%)
		24	27	30	18	21	24		
1. Dry-Matter Production (g)	ET[b]	2.302	3.616	2.705	3.416	2.502	2.705	2.874	(1) 1.031
	EM	5.633	6.726	5.339	5.589	6.251	5.858	5.899	(2) 1.785
	EL	7.578	7.661	6.037	6.704	7.353	7.219	7.092	
	Av.	5.171	6.001	4.694	5.236	5.369	5.260		
2. Stem Height (cm)	ET	22.83	26.28	35.97	30.57	28.13	26.38	28.36	(1) 6.60
	EM	58.27	60.33	69.77	60.50	64.30	63.57	62.79	(2) 11.43
	EL	46.22	52.92	63.93	39.10	62.38	61.58	54.36	
	Av.	42.44	46.51	56.56	43.39	51.61	50.51		
3. Stem Diameter (mm)	ET	3.92	4.55	4.23	4.48	4.17	4.05	4.23	(1) 0.65
	EM	5.20	5.20	5.03	5.43	5.10	4.90	5.14	(2) 1.12
	EL	5.53	5.03	4.85	4.97	5.30	5.15	5.14	
	Av.	4.88	4.93	4.71	4.96	4.86	4.70		
4. Mean Relative Growth Rate (g/g/wk)	ET	0.6311	0.6254	0.6257	0.6205	0.6466	0.6150	0.6274	(1) 0.0443
	EM	0.6991	0.7241	0.7198	0.7096	0.7263	0.7071	0.7143	(2) 0.0768
	EL	0.7582	0.7590	0.7748	0.7513	0.7890	0.7517	0.7640	
	Av.	0.6961	0.7028	0.7067	0.6938	0.7206	0.6913		
5. Leaf Area Ratio (sq.cm/g)	ET	138	134	141	139	139	135	138	(1) 39
	EM	162	159	182	172	174	157	168	(2) 68
	EL	254	191	211	190	208	259	219	
	Av.	184	161	178	167	174	184		
6. Specific Leaf Area (sq.cm/g)	ET	285	270	319	287	300	287	291	(1) 31
	EM	332	306	417	370	364	321	352	(2) 54
	EL	323	303	373	298	372	329	333	
	Av.	314	293	370	319	346	312		
7. Leaf Weight Ratio (g/g) Arcsin values	ET	0.4819	0.4854	0.4594	0.4856	0.4707	0.4695	0.4753	(1) 0.0389
	EM	0.4597	0.4718	0.4853	0.4620	0.5009	0.4538	0.4723	(2) 0.0673
	EL	0.4566	0.4758	0.4795	0.4744	0.4684	0.4689	0.4706	
	Av.	0.4657	0.4777	0.4746	0.4740	0.4799	0.4641		

TABLE 9.3 (Cont'd)

A : EXPERIMENT I (Cont'd)

Parameters		Day Temperature °C			Night Temperature °C			Prov. Av.	LSD[a] (5%)
		24	27	30	18	21	24		
8. Total Leaf Area (sq.cm.)	ET	366.67	544.00	446.00	546.50	402.17	408.33	452.00	(1) 187.01
	EM	926.00	1103.00	1125.67	1083.00	1170.00	936.33	1063.11	(2) 323.90
	EL	1246.00	1292.50	1236.83	1078.00	1446.67	1250.67	1258.78	
	Av.	858.89	980.50	936.50	902.17	1006.94	865.78		
9. Shoot:Root Ratio (g/g)	ET	3.621	4.160	4.010	4.209	3.900	3.682	3.930	(1) 1.043
	EM	5.656	6.031	7.405	5.590	6.322	7.181	6.364	(2) 1.807
	EL	4.584	5.388	6.614	5.194	5.546	5.846	5.529	
	Av.	4.620	5.193	6.010	4.998	5.256	5.569		

	D/N[c]	24/18°C	24/21	24/24	27/18	27/21	LSD[a] (5%)
10. Net Assimilation Rate (g/sq.cm/wk)	ET[b]	0.4043	0.4479	0.3596	0.3815	0.4096	(1) 0.0253
	EM	0.4072	0.4512	0.3334	0.5079	0.4404	(2) 0.0442
	EL	0.3457	0.4186	0.3869	0.3425	0.4421	(3) 0.0766
	Av.	0.3857	0.4392	0.3600	0.4106	0.4307	
	D/N	27/24°C	30/18	30/21	30/24		Prov. Av.
	ET	0.3313	0.4281	0.4400	0.3693		0.3806
	EM	0.3706	0.4947	0.4012	0.3805		0.4208
	EL	0.3408	0.3676	0.3889	0.3924		0.3294
	Av.	0.3476	0.4302	0.4100	0.3808		

(a) LSD (5%) values for (1) Provenance (P), Day (D) and Night (N) Temperatures, (2) P x D, Px N, D x N and (3) P x D x N.

(b) Provenances: Low altitude provenance (EL) 570 m, Middle altitude provenance (EM) 1554m and Top altitude provenance (ET) 2743m.

(c) Day/Night temperatures (°C).

TABLE 9.3 (Cont'd)

B : EXPERIMENT II - Low Temperature Range

Parameter	D/N[b]	15/10	18/10	18/18	21/10	21/15	21/18	24/18	24/21	Av.	LSD[a](5%)
1. Dry-Matter Production (g)	ET[c]	0.1098	0.1412	0.4696	0.5917	0.5444	0.5415	1.3808	0.7453	0.5655	(1) 0.1736
	EM	0.0482	0.0609	0.4235	0.5614	0.4986	0.8191	0.5959	0.9927	0.5001	(2) 0.2835
	EL	0.0679	0.1027	1.0990	0.6500	0.7312	1.5348	2.1754	1.5114	0.9841	(3) 0.4910
	Av.	0.0753	0.1016	0.6640	0.6010	0.5914	0.9651	1.3840	1.0831		
2. Mean Relative Growth Rate (g/g/wk)	ET	.3870	.5013	.5227	.6120	.6185	.6944	.6871	.6518	.5844	(1) 0.0440
	EM	.4956	.5214	.7393	.6682	.7668	.8257	.8543	.8541	.7157	(2) 0.0719
	EL	.4581	.5118	.7769	.6953	.7557	.8567	.8892	.8405	.7230	(3) 0.1246
	Av.	.4469	.5115	.6796	.6585	.7137	.7923	.8102	.7821		
3. Stem Height (cm)	ET	2.6	2.9	6.7	5.9	7.0	7.5	13.4	8.6	6.8	(1) 1.65
	EM	2.7	2.5	8.1	7.2	8.0	16.0	13.1	18.0	9.4	(2) 2.69
	EL	2.4	3.0	9.0	7.3	9.8	20.7	20.8	14.7	11.0	(3) 4.65
	Av.	2.6	2.8	7.8	6.8	8.3	14.7	15.8	13.8		
4. Stem Diameter (mm)	ET	1.2	1.2	2.3	2.0	2.2	2.2	3.4	2.9	2.3	(1) 0.2
	EM	0.8	0.9	1.9	2.1	1.9	2.5	2.5	2.7	1.9	(2) 0.4
	EL	0.9	1.0	2.7	1.9	2.1	3.2	3.6	3.1	2.2	(3) 0.6
	Av.	1.0	1.0	2.3	2.0	2.1	2.6	3.1	2.9		
5. Mean Net Assimilation Rate (g/sq.cm/wk)	ET	.2248	.2788	.2657	.3698	.3015	.3437	.3404	.3037	.3045	(1) 0.0254
	EM	.2235	.2227	.3135	.3047	.2940	.2999	.2900	.2977	.2807	(2) 0.0415
	EL	.2287	.2267	.3077	.3639	.2993	.3358	.3290	.2838	.2969	(3) 0.0719
	Av.	.2257	.2427	.2956	.3461	.2995	.3277	.3198	.2951		
6. Leaf Area Ratio (sq.cm/g)	ET	186.95	195.54	199.32	201.07	210.56	207.42	210.25	215.47	203.32	(1) 8.06
	EM	280.63	288.37	303.19	286.62	314.48	326.25	306.93	323.53	303.75	(2) 13.16
	EL	255.24	282.97	288.31	232.14	282.74	294.46	286.53	299.49	277.73	(3) 22.80
	Av.	240.94	255.63	263.61	239.94	269.26	276.04	267.90	279.50		

TABLE 9.3 (Cont'd)

B : EXPERIMENT II (Cont'd)

Parameter	D/N[b]	15/10	18/10	18/18	21/10	21/15	21/18	24/18	24/21	Av.	LSD[a](5%)
7. Specific Leaf Area ($sq.cm/g \times 10^{-2}$	ET	18.44	17.69	13.48	13.56	13.54	13.78	10.34	13.43	14.28	(1) 2.49
	EM	24.78	21.25	20.59	16.59	24.53	20.19	16.61	13.29	19.73	(2) 4.06
	EL	21.24	26.99	15.77	13.69	18.18	13.48	13.17	13.53	17.01	(3) 7.04
	Av.	21.48	21.98	16.62	14.61	18.75	15.82	13.37	13.42		
8. Leaf Weight Ratio ($g/g \times 10^{2}$ Arcsin	ET	54.50	53.18	52.87	52.66	51.04	53.22	50.15	52.71	52.54	(1) 1.14
	EM	50.93	50.66	51.51	49.35	50.55	51.72	48.74	48.98	50.31	(2) 1.87
	EL	49.15	51.00	49.81	51.17	52.29	48.59	49.93	48.80	50.10	(3) 3.23
	Av.	51.53	51.61	51.40	51.06	51.29	51.18	49.61	50.17		
9. Total Leaf Area (sq.cm)	ET	14.97	21.51	78.14	97.83	98.82	96.46	250.77	145.75	100.53	(1) 41.30
	EM	10.42	13.99	113.44	125.87	140.14	240.99	163.43	290.61	137.36	(2) 67.44
	EL	14.51	27.07	287.72	109.57	206.47	437.59	595.56	456.01	266.81	(3)116.81
	Av.	13.30	20.86	159.77	111.09	148.47	258.35	336.59	297.46		
10. Shoot:Root Ratio (g/g)	ET	2.8724	2.6892	3.1388	3.0665	2.9310	3.4120	3.4000	3.5178	3.1730	(1) 0.2449
	EM	2.3927	2.5678	2.8969	2.4592	2.4683	3.3510	2.6901	3.8855	2.8389	(2) 0.3999
	EL	2.0939	2.4153	3.3528	2.7049	3.5308	3.6144	3.8998	3.7724	3.1285	(3) 0.6926
	Av.	2.4530	2.5374	3.1295	2.7435	2.9767	3.4590	3.3300	3.7253		

(a) LSD (5%) values for (1) Provenance (P), (2) Temperature treatments (T) and (3) P x T.

(b) Day/Night temperatures (^{o}C) (c) Provenances as in Experiment I.

TABLE 9.4 Summary of Analysis of Variance (Type II) of Various Growth Parameters of *E. decaisneana* Seedlings from Three Altitudes Grown Under Two Ranges of Day x Night Temperatures: High Temperature Range in Experiment I and Low Temperature Range in Experiment II. Only Mean Square Values Given.

1. All analysis was conducted on final harvest data of 80 day old seedlings following 54 days of treatment. Exceptions were the ages of seedlings used in the calculation of mean RGR and NAR (refer Methods).

2. Significance levels: *5%, **1% and ***0.1%.

TABLE 9.4 (Cont'd)

I. GROWTH AND PRODUCTIVITY

Source of Variation	DF	Dry-Mat. Prod. (g)	Stem Height (mm)	Stem Diam. (mm)	DF	Mean Relative Growth Rate (g/g/wk)
A. High Temperature Range						
1. Prov. (P)	2	42.543***	289,816***	2.475*	2	0.1291***
2. Day T (D)	2	3.937(*)	47,513**	0.124	2	0.0008
3. Night T(N)	2	0.045	17,916*	0.155	2	0.0071
4. P x D	4	0.766	838	0.290	4	0.0008
5. P x N	4	0.665	18,520*	0.148	4	0.0003
6. D x N	4	1.700	8,118	0.337	4	0.0014
7. P x D x N		-	-	-	8	0.0029
8. Error	8	0.896	3,671	0.353	54	0.0022
B. Low Temperature Range						
1. Prov. (P)	2	1.6548***	10,910***	0.999**	2	0.2435***
2. Temp. (T)	7	1.8694***	24,147***	5.821***	7	0.2658***
3. P x T	14	0.2785**	2,356**	0.246(*)	14	0.0098(*)
4. Error	48	0.0895	804	0.147	96	0.0096

II. ANALYSIS OF PRODUCTIVITY

	DF	Leaf Area Ratio (sq.cm/g)	Specific Leaf Area (sq.cm/g)	Leaf Wt. Ratio (g/g)x10^2	DF	Mean Net Ass. Rate (g/sqcm/wk)
A. High Temperature Range						
1. Prov. (P)	2	15,195**	8,648**	0.477	2	0.0111**
2. Day T (D)	2	1,307	14,161**	2.472	2	0.0012
3. Night T (N)	2	660	2,860	1.977	2	0.0294***
4. P x D	4	1,147	1,722	2.619	4	0.0034
5. P x N	4	1,754	1,839	3.734	4	0.0110**
6. D x N	4	1,316	421	2.084	4	0.0160***
7. P x D x N		-	-	-	8	0.0107***
8. Error	8	1,291	812	3.552	54	0.0022
	DF	(unit) x 10^{-2}	(unit) x 10^{-2}	(g/g) x 10^2 Arcsin Val.	DF	
B. Low Temperature Range						
1. Prov. (P)	2	6.5201***	178.03***	44.0967***	2	0.0059*
2. Temp. (T)	7	0.2010***	104.34***	4.5829	7	0.0254***
3. P x T	14	0.0341	18.68	4.9266	14	0.0023
4. Error	48	0.0193	18.40	3.8824	96	0.0032

TABLE 9.4 (Cont'd)

III. LEAF AREA AND SHOOT:ROOT RATIO

	DF	Total Leaf Area (sq.cm)$\times 10^{-3}$	Shoot:Root Ratio (g/g)
A. High Temperature Range			
1. Prov. (P)	2	1591***	13.763**
2. Day T (D)	2	34	4.387*
3. Night T (N)	2	48	0.738
4. P x D	4	8	0.761
5. P x N	4	57	0.847
6. D x N	4	78	0.295
7. Error	8	29	0.917

	DF	(sq.cm)	
B. Low Temperature Range			
1. Prov. (P)	2	183,054***	0.7897*
2. Temp. (T)	7	131,935***	1.8081***
3. P x T	14	25,884***	0.3270
4. Error	48	5,066	0.1781

FIGURE 9.1 Multiple Range Test of Means of Growth Parameters of *Eucalyptus decaisneana* Seedlings Grown Under Two Ranges of Day x Night Temperatures: High Temperature Range in Experiment I and Low Temperature Range in Experiment II. Relative Values Given.

1. Growth parameters: Means of all growth parameters were calculated from final harvest data of 80 day old seedlings following 54 days of treatment. Exceptions were the calculations of mean RGR and NAR (refer Methods).

2. Ranking of means: In descending order from biggest at the top to smallest at the bottom.

3. Duncan's multiple range test: Means not connected by vertical line are significantly different at 5% level.

FIGURE 9.1 (Cont'd)

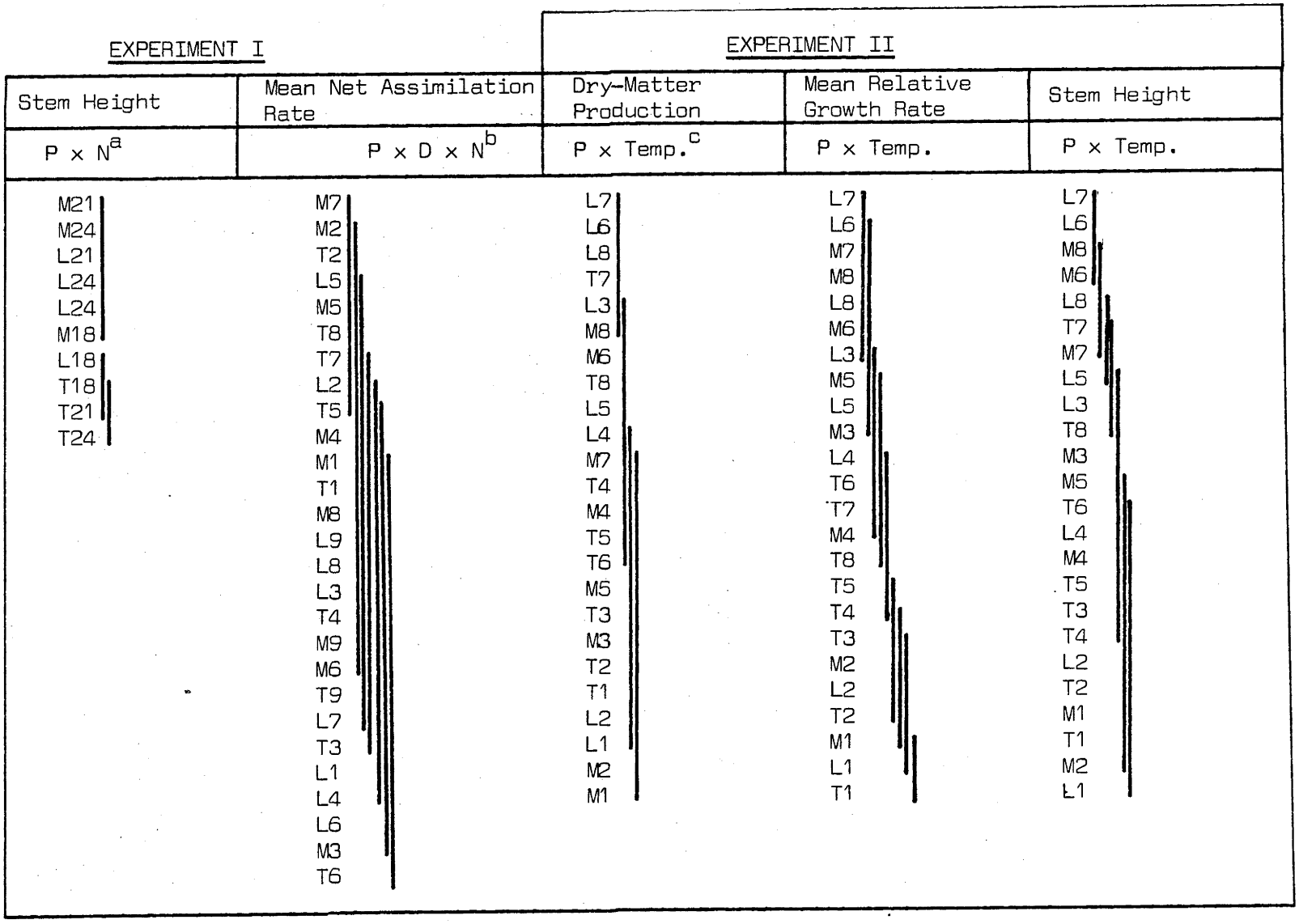
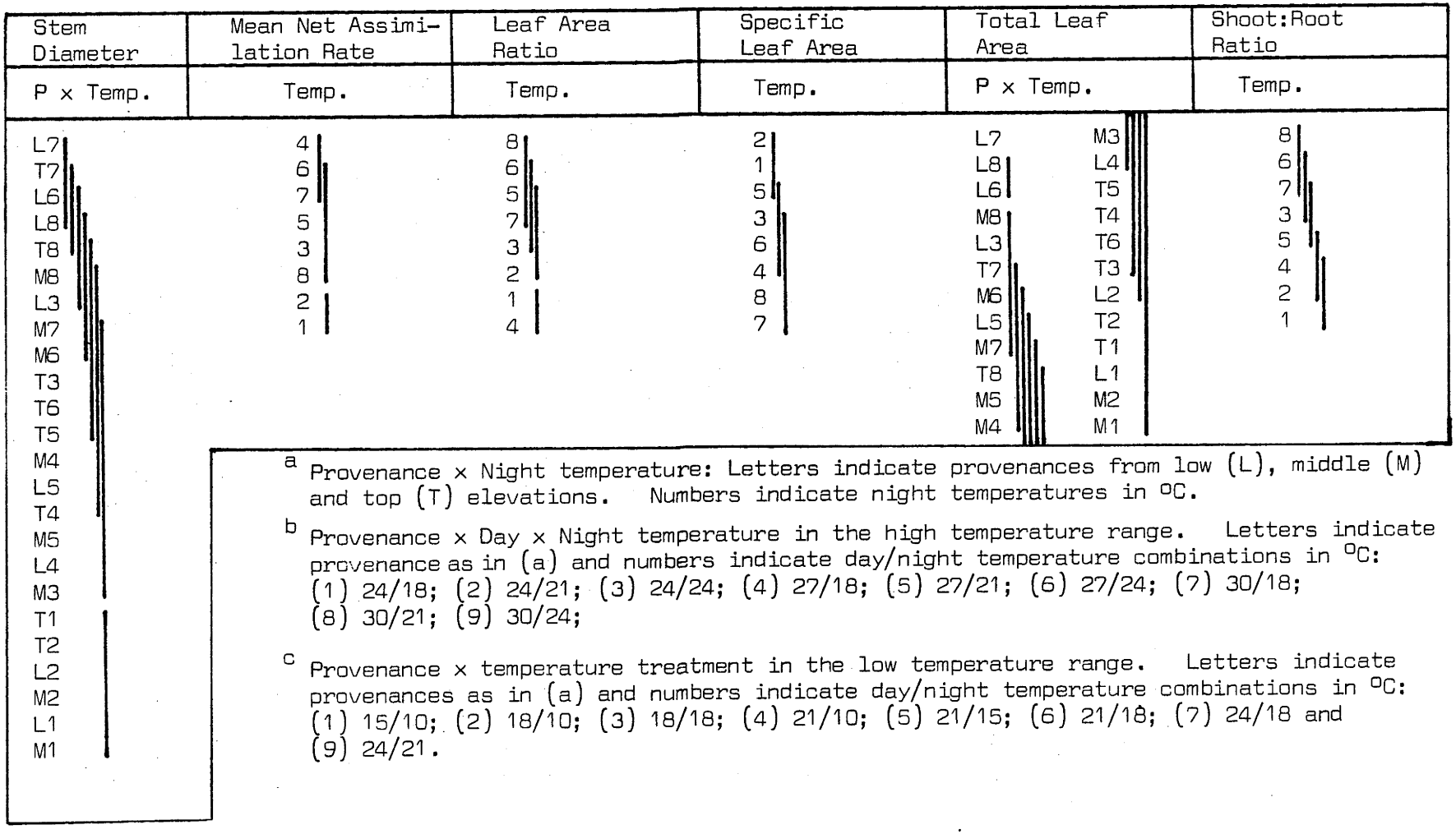


FIGURE 9.1 (Cont'd)

EXPERIMENT II (Cont'd)



[a] Provenance x Night temperature: Letters indicate provenances from low (L), middle (M) and top (T) elevations. Numbers indicate night temperatures in °C.

[b] Provenance x Day x Night temperature in the high temperature range. Letters indicate provenance as in (a) and numbers indicate day/night temperature combinations in °C: (1) 24/18; (2) 24/21; (3) 24/24; (4) 27/18; (5) 27/21; (6) 27/24; (7) 30/18; (8) 30/21; (9) 30/24;

[c] Provenance x temperature treatment in the low temperature range. Letters indicate provenances as in (a) and numbers indicate day/night temperature combinations in °C: (1) 15/10; (2) 18/10; (3) 18/18; (4) 21/10; (5) 21/15; (6) 21/18; (7) 24/18 and (9) 24/21.

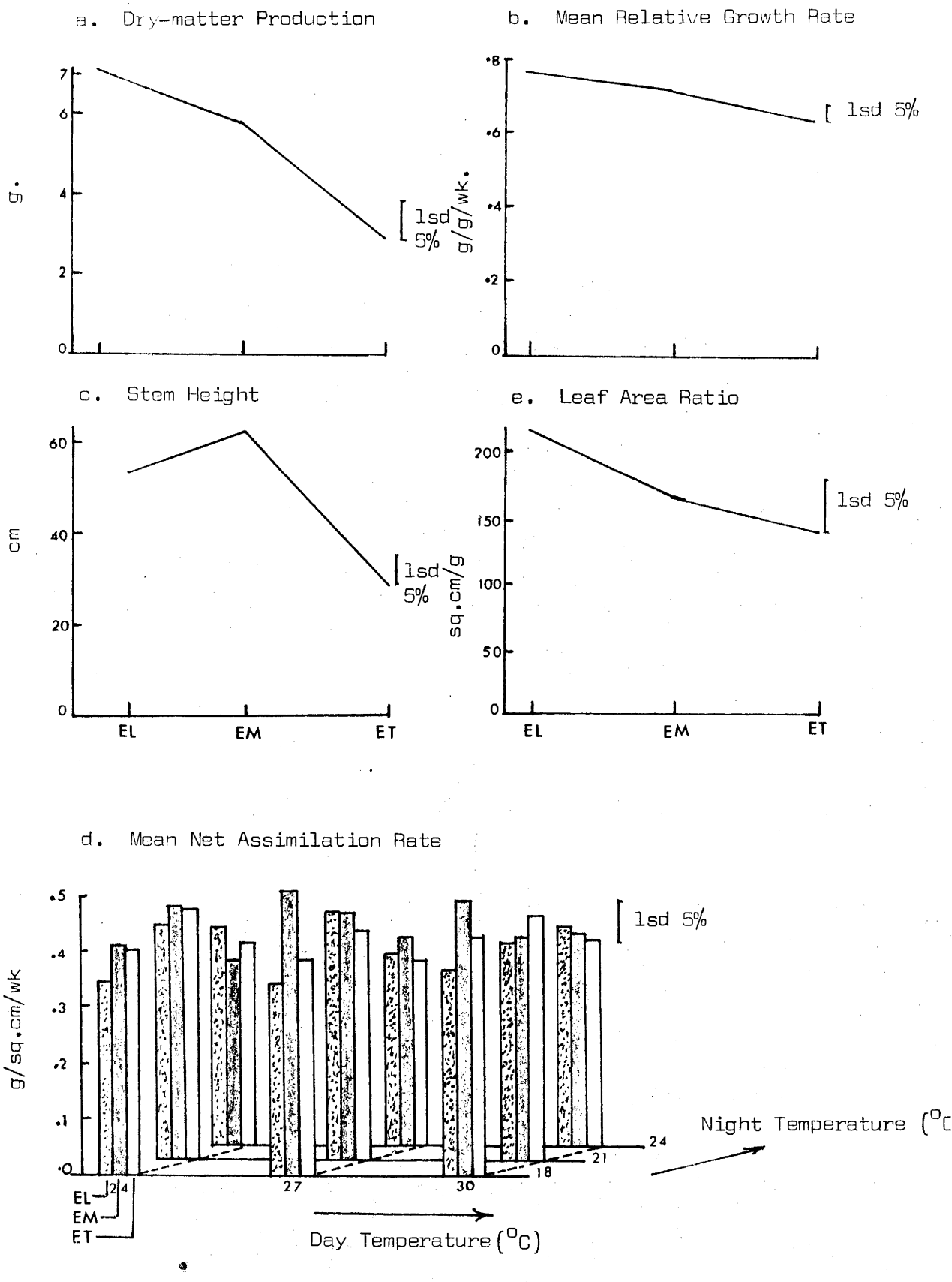


FIGURE 9.2 Growth Response of Seedlings of Eucalyptus decaisneana to Varying Day and Night Temperatures. I. High Temperature Range (Day/Night Temperature (°C): 24/18-30/24). Seedlings Grown from Low (EL), Middle (M) and High (ET) Altitude Sources

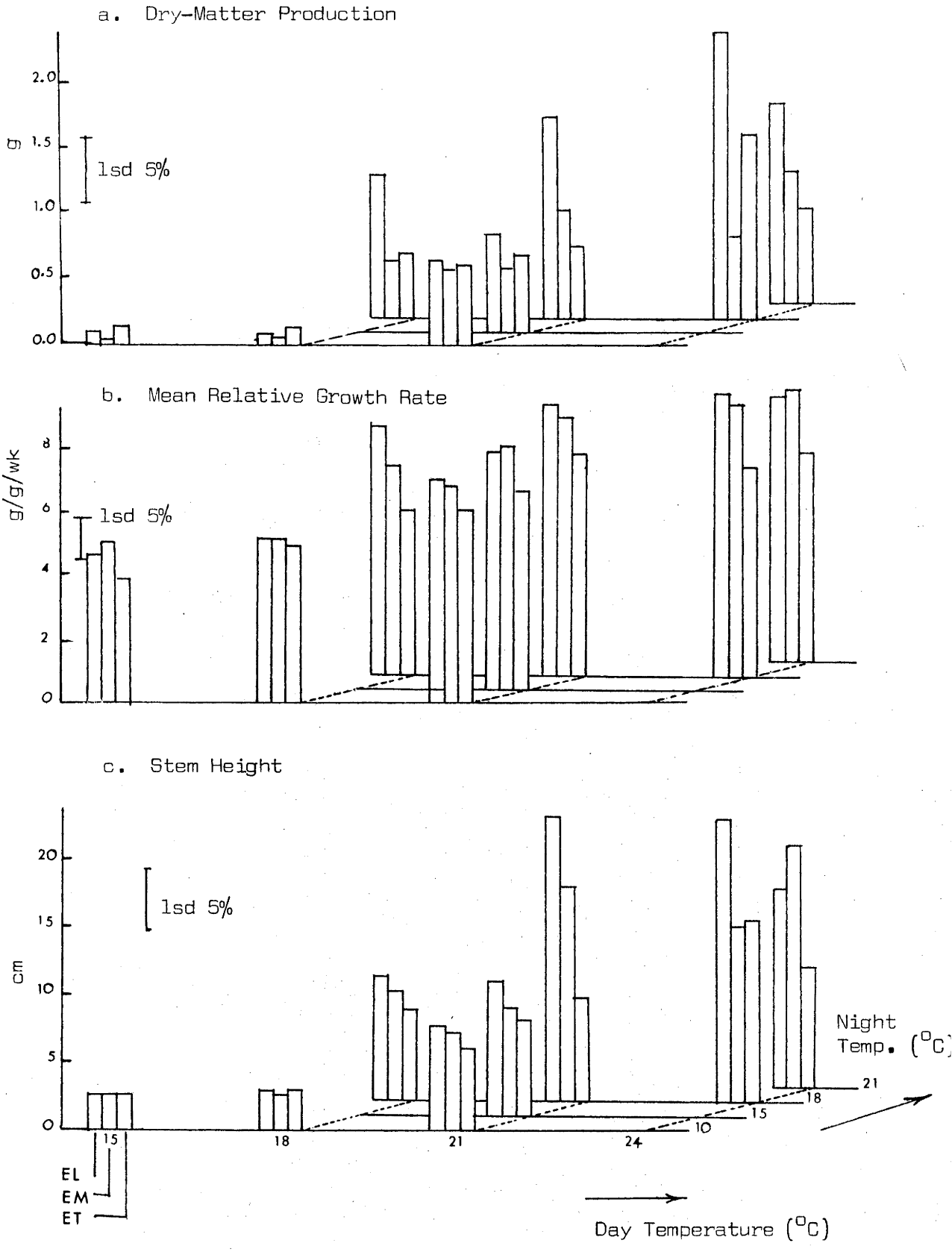
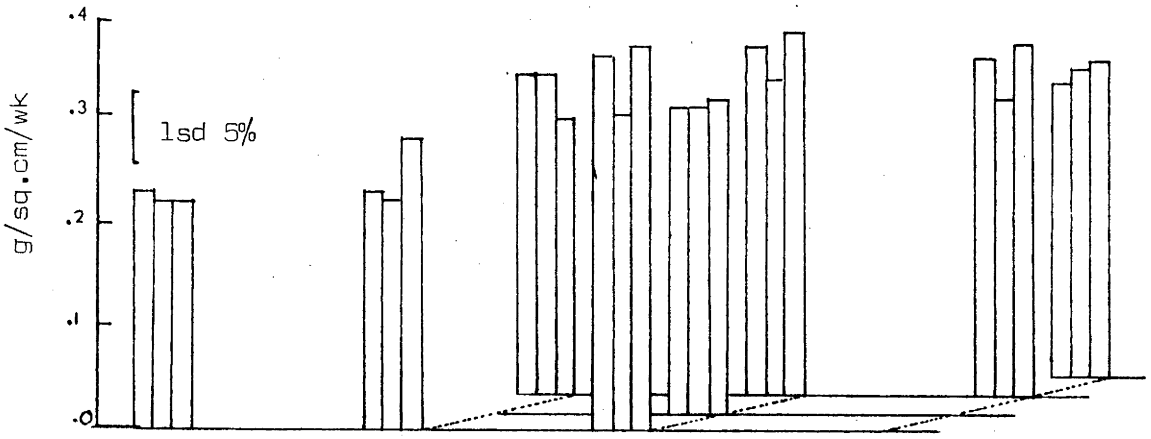
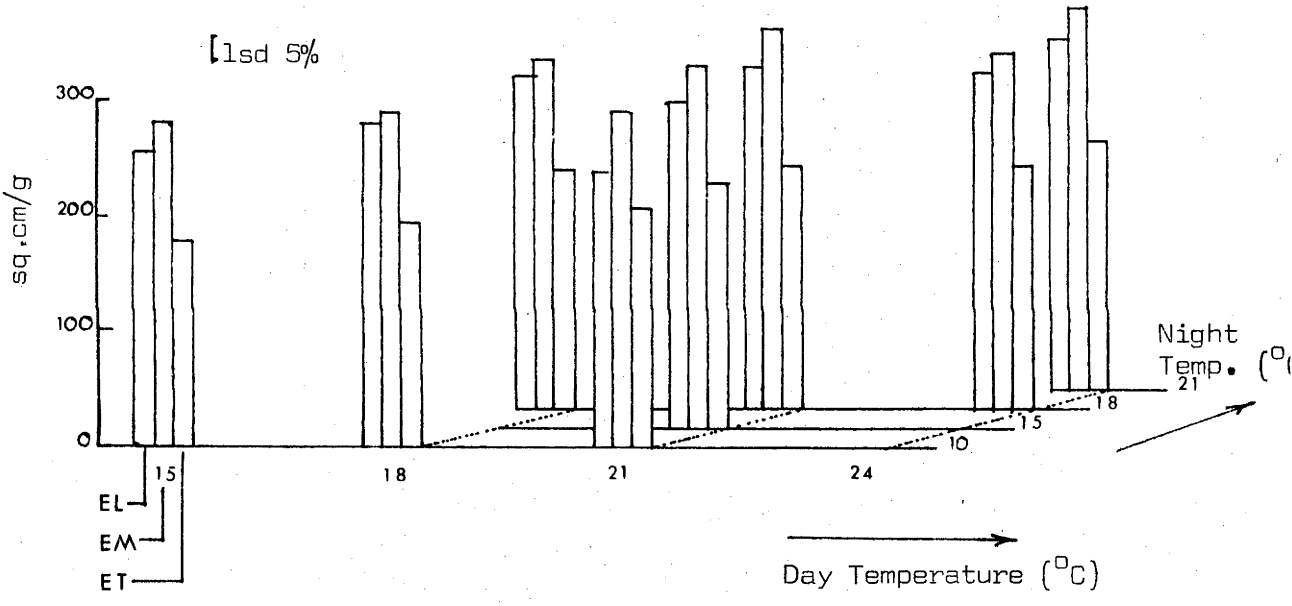


FIGURE 9.3 Growth Response of Seedlings of Eucalyptus decaisneana to Varying Temperatures. II. Low Temperature Range (Day/Night Temperature (°C): 15/10-24/18). Seedlings Grown from Low (EL), Middle (EM) and High (ET) Altitude Sources

d. Mean Net Assimilation Rate



e. Leaf Area Ratio



Provenance differences in growth rate and dry-matter production occur in all temperatures except those with cold night regimes (below 18°C), Figure 9.3a. The low provenance seedlings (EL) were generally the fastest growing and the most productive although at the lower temperatures the middle altitude seedlings (EM) had comparable growth rate (Figure 9.3b) and at 24/21°C also comparable productivity (Figure 9.1).

The high altitude seedlings (ET), in contrast to the lower provenances (EL and EM), had the lowest growth rate. Produtivity in ET was also smallest under higher temperatures but slightly better than that of EM under lower temperatures, significantly so at 24/18°C (Figure 9.3a).

An altitudinal trend in stem growth was however less clear. Although EM seedlings were tallest under higher temperatures (Figure 9.2c) they were generally slightly shorter than EL seedlings at the lower temperatures, significantly at 24/18°C, Figure 9.3c. ET seedlings, in contrast, had generally the poorest height growth except under some regimes where stem height was comparable with that of other provenances: For example, at 18°C night temperature in Experiment I and at 24/18°C in Experiment II Figures 9.1, 9.3c.

At higher temperatures, stem diameter between the lower provenances (EL and EM) was similar but decreased with elevation (Table 9.2). The altitudinal pattern was not maintained at lower temperatures where diameter was smallest in the middle altitude provenance (EM).

(b) Analysis of Productivity

Altitudinal differences in net assimilation rate (NAR) and leaf area ratio (LAR) were not generally clinal, except for LAR at the higher temperatures (Experiment I). It can however be shown that altitudinal variations in growth rate were primarily a function of variations in the photosynthetic system as indicated by LAR. This relationship was clear at the higher temperatures. For example EL, despite its high productivity had a low NAR especially at the 18°C night temperatures (Figures 9.1, 9.2d). This was however offset by a high LAR value (Figure 9.2e). Interestingly, NAR and LAR of the upper provenances (EM and ET) were generally comparable. However, the greater growth rate in EM may be attributed to gerater NAR under certain temperatures - mainly, warm days and cool night (27/18°C and 30/18°C), Figure 9.1.

At lower temperatures (Experiment II), the low growth rate in the top provenance (ET) was mainly due to its relatively small LAR (Figure 9.3e) which largely offset its generally high NAR value (Figure 9.3d). Differences in growth rate between the lower provenances (EL and EM) were however due primarily to the slight differences in NAR.

(c) Analysis of the Photosynthetic System

Altitudinal variations in the photosynthetic system, (as indicated by LAR) was mainly determined by variations in specific leaf area (SLA). For example, the relatively low LAR in ET (Figures 9.2e, 9.3c) was due to low SLA, since its leaf weight ratio (LWR) was either

similar to (Experiment I) or significantly greater than (Experiment II) LWR's of the lower provenances (EL and EM), Table 9.1.

Leaf area decreased with elevaltion being greatest in the low altitude provenance (EL), especially under regimes with night temperatures warmer than 15^{o}C (Figure 9.1).

(d) Shoot:Root Ratio

At warmer temperatures, relative shoot growth was smaller in the top provenance (ET) than in lower provenances (EL and EM) (Table 9.3). The altitudinal cline was not maintained at lower temperatures where EM had significantly lower shoot:root ratio than the other provenances (EL and ET).

(e) Summary

1. Growth and Productivity

Growth and productivity in E. decaisneana generally decreased with elevation. The trend was however more marked in dry-matter production and growth rate than in stem growth. It was also more marked at the higher than at the lower temperatures.

2. Analysis of Productivity

Altitudinal variations in productivity in E. decaisneana was mainly due to variations in the photosynthetic system (indicated by LAR) and to a lesser extent due to variations in NAR.

3. Analysis of the Photosynthetic System

(i) Altitudinal variations in the photosynthetic system (LAR) in E. decaisneana were primarily determined by variations in SLA.

(ii) Leaf area decreased with elevation. The trend was more marked at higher than at lower temperatures.

4. Shoot Root Ratio

Relative shoot growth under warmer temperatures was greater at lower than at upper elevations. There was no altitudinal trend at the lower temperatures.

9.3.3 Temperature Differences

(a) Growth and Productivity

In the higher temperature range (Experiment I), dry-matter production was optimum at the 27°C day temperature and reduced significantly at 30°C (Table 9.3). Productivity was not significantly affected by night temperatures although the lower provenances (EL and EM) tended to grow better under warmer night (21°C) than the top provenance (18°C).

In the lower temperature range (Experiment II) productivity was generally high under the regimes common to both experiments (24/18 and 24/21°C) and low under the colder regimes, particularly those with cold nights (15 and 10°C). EL and ET grew best at 24/18°C whereas EM grew best under a warmer night temperature (24/21°C), Figure 9.3a. Further, the temperature range for high dry-matter production was relatively wide for EM (Figure 9.1).

Results from the multiple regression analysis suggest that day temperature was more important than night temperature in influencing dry-matter production in the lower temperature range tested (Experiment I). The standard partial regression coefficients for day and night

temperature were 0.4409 and 0.3120 respectively. Day (D) and night (N) temperatures were well correlated (R = 0.687) with plant dry weight (W) in the regression equation, W = 0.887D + 0.0439N - 1.7711.

Growth rate was less affected by temperature variation than dry-matter production (Table 9.2b), especially at the higher temperatures (Experiment I) where no significant variation occurred. This pattern was also generally evident in the warmer regimes (above 21/10^{o}C) of the low temperature range (Experiment II).

Height growth was highly responsive to temperature variation in contrast to growth rate and dry-matter production. At the higher temperatures, height increased significantly with day temperature increase (24 to 30^{o}C), Table 9.3. As with dry-matter production, height growth was not significantly affected by night temperature except for the sensitivity of EL to cool night temperature (18^{o}C), Figure 9.1. At the lower temperatures height growth was generally best in the warmer regimes (21/18^{o}C and above) where EM showed better growth under warmer temperature (24/21^{o}C) than the other provenances (24/18^{o}C), Figure 9.3c. Interestingly, height growth in EL was depressed under the warmest temperature (24/21^{o}C).

Diameter growth showed similar temperature response to growth rate with little change over the higher temperature ranges (Experiment I) and warmer treatments of Experiment II.

(b) Analysis of Productivity

Photosynthetic efficiency (as indicated by NAR) was highly variable in the higher temperature range (Experiment I). Provenance x

day x night interaction was significant at 0.1% level, Table 9.4. EL was most efficient under warmer temperatures (27 and 30°C day x 21 and 24°C night temperatures), EM under warmer days and cold night (27 and 30°C day x 18°C night) and ET under cooler temperatures (24°C day x 18 and 21°C night). At the lower temperatures (Experiment II) the provenances were more efficient under day temperatures warmer than 18°C - especially at 21/10, 21/18 and 24/18°C (Figure 9.1).

Temperature response of LAR generally paralleled the response for growth rate. For example, in the higher temperature range there was no variation in LAR, Table 9.3. At the lower temperatures, temperature regimes maximum for growth rate also produced maximum LAR - mainly, 21/18, 24/18 and 24/21°C. LAR was less responsive to temperature changes than NAR.

Both NAR and LAR were generally influential in determining growth rate in the higher temperature range (Experiment I). The difference in growth rate between 24/18 and 24/21°C for example, was due to the increase in NAR and LAR (Table 9.4). Growth rate was similarly determined in the warmer regimes of the low temperature experiment. However, in the colder regimes, NAR appeared more influential. For instance, the increase in growth rate between 18/10 and 18/18°C (Figure 9.3b) was due to and increase in NAR (Figure 9.3d) which offset a decrease in LAR (Figure 9.3e).

(c) Analysis of the Photosynthetic System

Variations, with temperature, in the photosynthetic system (as indicated by LAR) was due to variations in both SLA and LWR. For example, the change in LAR between 30/18 and 30/21°C in the higher

temperature range (Experiment I) and between 24/18 and 24/21°C at the lower temperatures (Experiment II) was due to an increase in both SLA and LWR (Table 9.3).

(d) Shoot:Root Ratio

Distribution of dry matter to the shoot system was generally favoured by an increase in temperature. At warmer temperatures (Experiment I), the elevation in day temperature from 24 to 30°C increased relative shoot weight significantly (Table 9.3). At the lower temperatures (Experiment II) relative shoot weight was greater in the warmer regimes than in the colder regimes (Figure 9.1).

(e) Summary

(i) Growth and Productivity

Dry-matter production was optimum at 27°C day temperature in combination with 18-24°C night temperatures. Generally day temperature variations were more influential on dry-matter production than night temperature variations.

Growth and productivity were generally promoted by warmer temperatures with night regimes above 10 to 15°C within the range of temperatures tested (15/10 to 30/24°C).

(ii) Analysis of Productivity

There were large intraspecies differences in NAR response to temperature variations at the higher temperatures (ExperimentI) but not at the lower temperatures (Experiment II). In contrast, LAR exhibited little response to temperature changes.

Variations in growth rate with temperature were generally determined by variations in both NAR and LAR. However, under colder regimes at the lower temperatures (Experiment II) NAR appeared more influential.

(iii) Analysis of the Photosynthetic System

Variations in LAR (a measure of the photosynthetic system) was generally determined by variations in both SLA and LWR.

(iv) Shoot:Root Ratio

The proportion of dry matter distributed to the shoot system generally increased with the increase in temperature.

9.4 DISCUSSION

Differences in growth performance in seedlings grown under common temperature regimes (21/18 and 24/21^{o}C) between the high and low temperature experiments (Experiments I and II respectively) has already been noted (Section 9.3.1) and ascribed to the possible variation in daylight intensity. The results of the study are therefore tentative and subject to confirmations by further investigations.

The existence of intraspecies differentiation within E. decaisneana, the role of temperature in determining intraspecies distribution and the application of results of study are discussed.

9.4.1 Intraspecies Differentiation in E. decaisneana

It is clear from the experiment that intraspecies differences occur within E. decaisneana. This is evident from the significant provenance differences in nearly all the parameters measured (Table 9.4).

Growth rate and dry-matter production exhibited a significant reduction with elevation of provenance - a pattern generally associated with highland vegetation in the tropics (e.g. Brown, 1919). The strong altitudinal cline in productivity may be due to the long term conditioning of local ambient air temperature on growth rate. Plants growing at higher elevations are normally subjected to longer priods of sub-optimal temperatures for metabolic activity (e.g. Gates, 1969), in contrast to those growing at lower elevations.

In consequence, the reduction in growth rate with elevation usually occurs among highland species (Wadsworth and Bonnet, 1951).

Interestingly, all provenances grew best at the same temperatures and there was no evidence of the higher provenance (ET) requiring lower temperature for optimum growth. The optimum temperature (i.e., 24/18 to 30/24^{o}C) probably occur at all source elevations (see Appendix IV). Nevertheless the seasonal duration of this optimal temperature range probably decreased with altitude.

It may however be noted that temperature may not be the only factor determining growth rate of altitudinal species. Its effects, although basic, may be indirect or modified by a large number of other environmental factors including light intensity, fog and soil nutrient (e.g. Grubb, 1971).

The plant factors controlling growth rate and productivity vary according to altitude and temperature. For example, at higher temperatures (Experiment I), the high growth rate of EL was due primarily to its high LAR (Figures 9.2b, e). Similarly, the low growth rate in ET at the lower temperatures (Experiment II) was due

to a small LAR (Figures 9.3b, e). In contrast, at the lower temperatures differences in NAR appeared important in determining the growth rate differences between the lower provenances (EL and EM).

Another example of intraspecies differentiation was the higher photosynthetic efficiency (as indicated by NAR) of the high altitude provenance (ET), especially at the lower temperatures (Experiment II). Under colder regimes efficiency in energy utilisation appeared important in determining growth rate (Section 9.3.3b). Since temperatures of this order are generally associated with higher elevations the photosynthetic efficiency in ET may indicate adaptation to these elevations. High altitude ecotypes are known for their efficiency in energy utilisation especially under conditions of wide temperature fluctuations (e.g. Wright, 1971).

9.4.2 Intraspecies Distribution in E. decaisneana

The E. decaisneana forest of Timor is a fire sub-climax, (Appendix IV) with fire being the primary determinant of natural distribution. Other environmental factors may however be important. The possible role of temperature in determining the intraspecies distribution of E. decaisneana is examined here.

The absence of different temperature optima for the different altitudinal provenances would suggest the provenances may potentially co-occur over a wide range of altitudes. Thus the presence of altitudinal segregation in E. decaisneana indicates that temperature alone may not be directly important in determining intra-species distribution of the species. It is probable that the lower limits of distribution of the upper provenances (EM and ET) are

determined by growth rate. For example, the upper provenances, with a slower growth rate, may be at a competitive disadvantage if grown at lower elevations with faster growing lower provenances. The possibility of plant competition in determining the lower limit of tropical highland vegetation has been suggested by Grubb (1971).

It should be noted however, that these suggestions are based on seedling materials. The factors controlling distribution may be entirely different. For example, temperature may have no apparent effect on the vegetative growth of seedlings but can have a role in delimiting species through an adverse influence on reproduction (van Steenis, 1971).

9.4.3 Application of the Results of Study

Evidence on the existence of altitudinal ecotypes in *E. decaisneana* as apparent from the study can be considered strong. In particular the low provenance (EL) consistently exhibited the best growth performance over the wide range of temperatures (15/10 to 30/24^{o}C). It is thus undoubtedly the most suitable choice for a plantation scheme, especially in view of its relatively high growth rate and productivity.

Whether the optimum temperature range suggested by the study has any field relevance is suspect. It can be reasonably suggested that the provenances perform better under warmer than under cooler temperatures. The conservative estimate of 24-27^{o}C day temperatures (maxima) and 18-24^{o}C night (minima) may be considered the optimum range for field projection.

It is however not possible to determine the upper altitudinal limit for good growth. The estimated critical low temperature for good growth (i.e. 15^{o}C night temperature) may suggest an upper limit of 1500m which lies within the Lower Montane Rain Forest zone. Considering the possible interaction of other important environmental factors on growth, such a projection cannot be made with certainty without further investigations.

Another area of application is in tree improvement. A fast growth rate and consequent high dry-matter production are desirable characters that are normally targeted in most breeding programmes. In E. decaisneana a fast growth rate is considered necessary to maintain its successional status in the face of competition from displaced rain-forest species. This is also an important consideration in the enrichment plantings of natural stands. It was apparent from the study that at lower elevations the photosynthetic system was considered the major determiner of growth rate. Consequently, in breeding for a fast growth rate, the improvement of the photosynthetic system should be given major importance.

CHAPTER 10

THE EFFECTS OF DAY AND NIGHT TEMPERATURE ON GROWTH OF SEEDLINGS OF PINUS OOCARPA SCHIEDE VAR OCHOTERENAI AND PINUS CARIBAEA VAR HONDURENSIS B AND G

10.1 INTRODUCTION

Pinus oocarpa Schiede is a very variable and wide-ranging species occurring from N-W Mexico in the north to Nicaragua in the south (Mirov, 1967; see Figure IVb in Appendix IV). The variety ochoterenai occurs in the southern part of the distribution including south Mexico and British Honduras.

Altitudinally, P. oocarpa ranges from about 300m to 2400m altitude. The species is therefore subjected to a wide difference of mean ambient temperature, estimated at c.10^{o}C using the universal temperature lapse rate of -0.5^{o}C/+100m altitude (Section 3.4.1).

The object of this experiment is to investigate whether intraspecies differences in growth performance due to altitude occur in seedlings of P. oocarpa when treated to a wide range of temperatures. For this purpose the variety ochoterenai was chosen and seed sources covering a wide altitudinal range were used. A seed source of Pinus caribaea var. hondurensis B and G from Nicaragua was also included in the experiment to complement the altitudinal range of the Oocarpa series (see Section 8.2).

10.2 MATERIALS AND METHODS

The experiments were conducted at CERES phytotron from seed materials supplied by the Forest Research Institute in Canberra. The seed lot numbers were S8557, S9596, S9713 and S8512.

Four altitudinal seed sources were used. One of *P. caribaea* var. *hondurensis* (PC) from 160m and three of *P. oocarpa*: Low altitude provenance (POL) from 380m, middle altitude provenance (POM) from 1000-1300m and high altitude provenance (POT) from 1770m elevation. Detailed origin of the seed sources had already been given (see Section 8.2 and Table 8.1).

The experiments conducted were identical with those for the Eucalyptus series (Section 8.4, Table 8.2). The treatments were therefore the same (refer Section 9.2). Briefly, in Experiment I, nine temperature combinations of three day (24^{o}, 27^{o} and 30^{o}C) and three night (18^{o}, 21^{o} and 24^{o}C) temperatures were used. The seed sources used were PC, POM and POT. In Experiment II, nine temperature regimes were used - 15/10, 18/10, 18/15, 18/18, 21/10, 21/15, 21/18, 24/18 and $24/21^{o}$C. Only two seed sources were however used; POL and POT. PC was excluded due to repeated germination failures. Supply of POM was exhausted and was duly replaced with POL from the same area of origin as POM but of lower altitude (Table 8.2).

Both experiments were conducted in 'C' cabinets. The growth conditions in these cabinets and routine maintenance are outlined in Sections 8.3 and 8.8.4.

It was rather difficult to determine whether the temperature regimes of both experiments adequately covered the natural temperature range of the source altitudes. Meteorological data obtained were fragmentary. The determination of the temperature regimes used was thus mainly by projections. The alignment of temperature treatments for both Eucalyptus and Oocarpa series was necessary due to the sharing of experimental space.

Seedling materials used were established and graded according to the standardised procedures outlined in Section 8.8.2 and 8.8.3. Their ages varied between 28 to 31 days at the commencement of treatment.

The harvesting schedule and corresponding average ages of seedlings are shown in Table 10.1. The dates of commencement of treatments varied between 1 to 5 days due to variation in germination times. In general, the treatment lasted 131 days. The average dates for the bulk of the experiment were 17/2/71 to 10/5/71 in Experiment I and 23/6/74 to 30/9/74 in Experiment II.

There were differences in harvesting schedule in Experiment I due to differences in growth rate between PC and oocarpa seedlings (Table 10.1). The Treatment duration of the PC seedlings was terminated earlier on the 101st. day owing to their fast growth rates. No harvest was made of oocarpa seedlings on the third harvest schedule since growth increment was considered small. They were allowed to grow till the 131st day before final harvest. In Experiment II more suitable seedlings and larger experimental space were available thus allowing for an additional harvest.

TABLE 10.1 Harvesting Schedule : Temperature Experiment with Oocarpa Series

Harvest Schedule	Age (days) since Treatment[a]			No. of Replicates[b]			Total No. of Replicates Harvested	
	I		II	I		II		
	PC	PO		PC	PO		I	II
1	49	49	49	1	1	1	27	16
2	62	62	62	1	1	1	27	16
3	89	-	89	1	-	1	9	16
4	101	101	101	3	1	1	45	16
5	-	131	131	-	1-3	3	26	48

a Treatment commenced at 28-31 days following germination

b Per provenance per treatment

I Experiment I

II Experiment II

The number of seedlings harvested initially varied between 10 to 20 according to the number available. In consequent harvests but the last, one seedling per provenance per treatment was harvested. In the final harvests three seedlings were harvested except for the oocarpa provenances in Experiment I where the number varied between 1 to 3 due generally to initial shortage of suitable seedlings. The total number of seedlings harvested totalled 134 and 112 in Experiments I and II respectively.

The parameters measured at each harvest were stem height and diameter, and the component oven dry weights of needles, stem, branches and root. From these the total plant dry weight, mean relative growth rate and net assimilation rate were calculated.

In the final harvests, branch number and length were additionally measured and shoot:root ratio and leaf weight ratio (as % needle weight) claculated. The measurement and calculation of parameters were as outlined in Sections 8.5 and 8.7.

The analysis of results was similar with that for the Eucalyptus series (Section 9.2). Analysis of variance (type II) was conducted on both primary and derived data. In the analysis of mean relative growth rate and net assimilation rate the averages of final harvests data measurement were used thus giving four replicates per provenance and treatment in Experiments I and five in Experiment II, totalling 108 and 80 replicates respectively. The calculation of the latter figure was based on eight treatments due to the loss of treatment $18^{o}/15^{o}C$ during experiment.

In Experiment I, the analysis of variance was in addition carried out on all primary and derived data (except component dry weights) of the fourth harvest (Table 10.1) which was common to all seed sources. Only average values of PC data were used, thus giving one replicate per provenance and treatment and totalling 27 replicates for the whole experiment. The analysis was conducted as for a balanced factorial design without replicate - 3 provenance x 3 day x 3 night temperatures.

In Experiment II similar analysis was conducted but on data of the fifth and final harvest with three seedlings per provenance and treatment giving a total of 48 replicates for the whole experiment. It was decided not to analyse harvest four data as in Experiment I. This was based on observed large differences found between the two experiments in height growth of POT seedlings, although raised under similar temperatures (24/18^{o} and 24/21^{o}C). Direct comparison of results of the two experiments was therefore not possible. In consequence, final harvest was extended to the 131st day to allow for greater provenance differences to develop further.

In Experiment II, it was not possible to seperate the day and night temperature effects due to the two factorial design (3 provenances x 8 treatments) in which both temperatures were integrated as one factor. Multiple regression analysis (Section 8.7.2c) was therefore conducted to evaluate their relative effects on dry-matter production.

10.3 RESULTS

Results of Experiments I and II are given in Table 10.2. Results of analysis of variance are summarized in Table 10.3 and means compared with Duncan's multiple range test given in Figure 10.1. The more important parameters are shown in Figures 10.2a-e, 10.3a-d.

10.3.1 Provenance Differences

(a) Growth and Productivity

Dry-Matter Production.

In the higher temperature range of Experiment I (24/18 to 30/24°C), P. caribaea seedlings (PC) were clearly the most productive of the species with dry-matter production nearly twice that of the oocarpa provenances (POM and POT), Figure 10.2a. A trend of decreasing productivity with altitude appears to exist within P. oocarpa although it was not significant. This was evident from the slightly lower dry-matter production in the top provenance (POT) relative to the middle provenance (POM) in the higher temperature range, and the low provenance (POL) in the low temperature range of Experiment II (15/10 to 24/18°C), Figures 10.1, 10.2a, 10.3a.

Relative Growth Rate

Growth rate in the high temperature range was significantly highest in POM whereas PC and POT had comparable values (Figure 10.2b). The clinal trend of decreasing growth rate with elevation in P. oocarpa was evident in the low temperatures where growth rate was slightly greater in POL than in POT (Figure 10.3b).

TABLE 10.2 Growth Response in Seedlings of *Pinus caribaea* and *Pinus oocarpa* Grown Under Two Ranges of Day x Night Temperatures: High Temperature Range in Experiment I and Low Temperature Range in Experiment II.

1. Means of all parameters were calculated from final harvest data of 132 day old seedlings following 101 days of treatment in Experiment I and of 162 day old seedlings following 131 days of treatment in Experiment II. Exceptions were calculations of mean RGR and NAR (refer Methods).

TABLE 10.2 (Cont'd)

EXPERIMENT I: High Temperature Range

Parameter		Day Temperature (°C)			Night Temperature (°C)			Average	L.S.D.[a] (5%)	
		24	27	30	18	21	24			
1. Plant Dry Weight (g)	POT[b]	2.854	2.840	3.419	3.024	2.884	3.205	3.038	(1)	0.791
	POM	3.262	3.008	3.074	3.865	3.015	2.464	3.115	(2)	1.370
	PC	7.002	5.476	5.190	6.218	6.048	5.402	5.889		
	Av.	4.737	3.775	3.894	4.369	3.982	3.690			
2. Mean Relative Growth Rate g/g/wk.	POT	.2697	.2722	.2689	.2715	.2630	.2760	.2702	(1)	0.0156
	POM	.2993	.3031	.3074	.3211	.2991	.2896	.3033	(2)	0.0269
	PC	.2920	.2868	.2797	.2889	.2855	.2840	.2862		
	Av.	.2870	.2874	.2853	.2939	.2826	.2832			
3. Stem Height (cm)	POT	25.03	26.93	32.47	27.57	26.30	30.57	**28.14**	(1)	3.95
	POM	27.25	32.23	37.03	34.10	32.85	29.57	**32.17**	(2)	6.84
	PC	36.17	32.73	41.16	36.21	36.44	37.40	**36.69**		
	Av.	29.48	30.63	36.89	32.63	31.86	32.51			
	Night									
	18	25.75	32.82	39.31						
	21	28.69	28.37	38.54						
	24	34.01	30.71	32.81						
4. Stem Diameter (mm)	POT	4.50	4.80	4.50	4.77	4.67	4.37	4.60	(1)	0.47
	POM	3.90	4.02	3.90	4.27	4.08	3.47	3.94	(2)	0.82
	PC	5.75	5.14	5.13	5.56	5.37	5.10	5.34		
	Av.	4.72	4.65	4.51	4.87	4.71	4.31			
5. Branch No.	POT	23.0	13.67	7.7	17.0	14.7	12.7	14.8	(1)	2.9
	POM	9.50	2.0	6.7	8.2	4.5	5.5	6.1	(2)	5.0
	PC	9.17	7.2	5.7	7.6	7.0	7.4	7.4		
	Av.	13.9	7.6	6.7	11.0	8.7	8.5			
6. Branch Length (cm)	POT	76.67	62.07	38.00	50.73	66.47	59.53	58.91	(1)	23.23
	POM	27.03	45.33	23.05	23.38	10.53	20.70	18.21	(2)	40.24
	PC	97.88	82.04	52.20	79.63	76.31	76.18	77.37		
	Av.	67.19	49.55	37.75	51.25	51.10	52.14			

TABLE 10.2 (Cont'd)

EXPERIMENT I: (Cont'd)

Parameter		Day Temperature (°C)			Night Temperature (°C)			Average	L.S.D.[a] (5%)
		24	27	30	18	21	24		
7. Shoot Root Ratio g/g	POT	4.500	3.764	5.183	3.414	4.532	5.500	4.482	(1) 0.651
	POM	3.190	3.795	3.837	3.622	3.301	3.900	3.607	(2) 1.127
	PC	2.946	3.136	3.296	3.176	3.260	2.942	3.126	
	Av.	3.545	3.565	4.105	3.404	3.698	4.114		
8. Leaf Weight Ratio $g/g \times 10^2$ (Arcsin)	POT	49.50	48.45	51.65	48.54	50.19	50.88	49.87	(1) 5.65
	POM	55.10	46.47	44.59	46.56	43.72	55.87	48.72	(2) 9.78
	PC	44.84	46.70	44.83	45.20	45.90	45.28	45.46	
	Av.	49.81	47.21	47.02	46.77	46.60	50.68		
9. Net Assimilation Rate g/g/wk.	D/N[c]	24/18	24/21	24/24	27/18	27/21	27/24		
	POT	.4226	.4347	.4648	.4410	.4116	.4802		(1) 0.0133
	POM	.5629	.5581	.4077	.5934	.5450	.5298		(2) 0.0230
	PC	.5086	.5127	.5112	.4947	.4579	.5062		(3) 0.0398
	Av.								
	D/N	30/18	30/21	30/24	Av. Prov.				
	POT	.4572	.4509	.4143	0.4416				
	POM	.6011	.5859	.5139	0.5442				
	PC	.4920	.4891	.4982	0.4967				
	Av.								

(a) LSD (5%) values for (1) Provenance (P), Day (D), Night (N) temperatures and (2) P x D, P x N, D x N.

(b) Species and provenances: P. caribaea (PC); P. oocarpa low altitude (POL) and Middle altitude (POM) provenances.

(c) Day/Night temperatures (°C).

TABLE 10.2 (Cont'd)

EXPERIMENT II: Low Temperature Range

Parameter	Day	15	18		21			24		Average	L.S.D.[a] (5%)	
	Night	10	10	18	10	15	18	18	21			
Plant Dry Weight (g)	POT[b]	.5394	.7826	2.1313	1.6483	2.0572	2.1404	2.7620	2.5945	1.8320	(1)	0.3367
	POL	.8581	.5996	2.7214	1.2613	1.9145	2.5749	2.7771	2.8364	1.9429	(2)	0.6735
	Av.	.6987	.6911	2.4263	1.4548	1.9859	2.3576	2.7695	2.7154		(3)	0.9524
Relative Growth Rate g/g/wk.	POT	.2125	.2012	.2998	.2503	.2735	.3064	.3154	.3477	.2759	(1)	0.0203
	POL	.1817	.2118	.3061	.2962	.3010	.3291	.3141	.3363	.2845	(2)	0.0406
	Av.	.1971	.2065	.3029	.2733	.2837	.3178	.3148	.3420		(3)	0.0574
Stem Height (cm)	POT	6.23	9.53	14.13	13.53	12.63	17.57	19.60	14.47	13.46	(1)	2.05
	POL	8.80	7.33	21.63	13.67	15.83	19.37	21.00	18.23	15.71	(2)	3.56
	Av.	7.52	8.63	17.88	13.30	14.23	18.47	20.30	16.35		(3)	5.81
Stem Diameter (mm)	POT	2.40	2.63	3.57	3.73	3.73	4.03	4.30	4.00	3.55	(1)	0.28
	POL	2.13	1.97	3.93	2.73	3.20	3.40	3.57	3.87	3.10	(2)	0.56
	Av.	2.27	2.30	3.75	3.23	3.47	3.71	3.93	3.93		(3)	0.79
Mean Net Assimilation Rate g/g/wk.	POT	.3545	.3236	.4604	.3985	.4233	.4626	.4846	.5308	.4298	(1)	0.0406
	POL	.3187	.3771	.5201	.5288	.5011	.5724	.5422	.5786	.4924	(2)	0.0812
	Av.	.3366	.3503	.4903	.4637	.4622	.5175	.5134	.5547		(3)	0.1148
Leaf Weight Ratio g/g x 10^2 (Arcsin)	POT	82.96	77.30	70.79	63.50	62.81	67.68	65.83	68.30	69.90	(1)	10.25
	POL	60.00	80.74	51.23	52.62	55.11	57.00	56.14	57.00	58.73	(2)	20.60
	Av.	71.48	79.02	61.01	58.06	58.96	62.34	60.98	62.65		(3)	29.14
Branch No.	POT	.67	4.00	13.67	10.33	10.33	10.33	8.67	7.00	8.13	(1)	2.09
	POL	.33	2.00	2.00	7.67	4.00	3.33	5.00	4.67	3.63	(2)	3.62
	Av.	.50	3.00	7.83	9.00	7.17	6.83	6.83	5.83		(3)	5.91
Branch Length (cm)	POT	0.47	9.47	36.00	27.00	23.30	41.00	41.07	23.23	25.19	(1)	7.18
	POL	0.23	5.23	10.00	14.93	16.90	20.10	23.33	21.33	14.01	(2)	14.36
	Av.	0.35	7.35	23.00	20.97	20.10	30.55	32.20	22.28		(3)	20.31
Shoot:Root Ratio g/g	POT	2.2703	2.6648	3.7315	3.0243	3.1946	3.8735	3.7711	2.6498	3.1475	(1)	0.2835
	POL	1.8257	2.1464	2.8936	1.8683	2.2330	2.4941	2.2578	2.2637	2.2478	(2)	0.4912
	Av.	2.0480	2.4056	3.3126	2.4463	2.7138	3.1838	3.0144	2.4567		(3)	0.8021

(a) LSD (5%) values for (1) Provenance; (2) Treatment; (3) Provenance x Treatment.

(b) P. oocarpa provenances as in Experiment I.

TABLE 10.3 Summary of Analysis of Variance (Type II) of Various Growth Parameters of *Pinus caribaea* and *Pinus oocarpa* Seedlings Grown Under Two Ranges of Day x Night Temperatures: High Temperature Range in Experiment I and Low Temperature Range in Experiment II. Only Mean Square Values Given.

1. All analysis was conducted on final harvest data of 132 day old seedlings following 101 days of treatment in Experiment I and of 162 day old seedlings following 132 days of treatment in Experiment II. Exceptions were the ages of seedlings used in the calculation of mean RGR and NAR (refer Methods).

2. Significance levels: *5%, **1% and *** 0.1%

TABLE 10.3 (Cont'd)

I: Growth and Productivity

A. High Temperature Range

Source of Variation	DF	Dry-Matter Production (g)	Stem Height (cm)	Stem Diameter (mm)	DF	Mean Relative Growth Rate (g/g/wk)
Prov. (P)	2	23.753***	16,430**	4.438***	2	0.0099***
Day Temp. (D)	2	0.901	14,280**	0.100	2	0.0000
Night Temp. (N)	2	1.044	152	0.731(*)	2	0.0015
P x D	4	1.164	1,377	0.189	4	0.0003
P x N	4	0.542	1,526	0.043	4	0.0012
D x N	4	0.342	5,189*	0.148	4	0.0015
P x D x N	-	-	-	-	8	0.0019
Error	8	0.527	1,315	0.183	81	0.0011
B. Low Temperature Range						
Prov. (P)	1	0.1477	6,052*	2.43***	1	0.0015
Temp. (T)	7	4.2998***	12,761***	2.81***	7	0.0277***
P x T	7	0.1719	1,190	0.27	7	0.0014
Error	32	0.3302	1,228	0.23	64	0.0020

TABLE 10.3 (Cont'd)

II: Analysis of Productivity

III: Branch Growth and Shoot:Root Ratio

A. High Temperature Range

	DF	Mean Net Assimilation Rate (g/g/wk)	DF	Leaf Weight Ratio $(g/g)\times10^2$	Branch Number	Branch Length Cumulative (mm)	Shoot:Root Ratio (g/g)
Prov. (P)	2	0.0944***	2	47	199.4***	824,768***	4.254**
Day Temp. (D)	2	0.0016	2	22	138.4***	197,612*	0.910
Night Temp. (N)	2	0.0068***	2	48	15.9	282	1.146
P x D	4	0.0058***	4	42	46.5	60,698	0.544
P x N	4	0.0150***	4	39	4.6	16,653	1.237
D x N	4	0.0052***	4	14	22.0	124,612*	0.188
P x D x N	8	0.0151***	–	–	–	–	–
Error	81	0.0008	8	27	7.0	45,522	0.357

B. Low Temperature Range

Prov. (P)	1	0.0015	1	1496*	243***	150,080**	9.7123***
Temp. (T)	7	0.0277***	7	312	47**	70,300**	1.1517***
P x T	7	0.0014	7	94	20	13,605	0.2778
Error	64	0.0020	32	306	13	15,012	0.2342

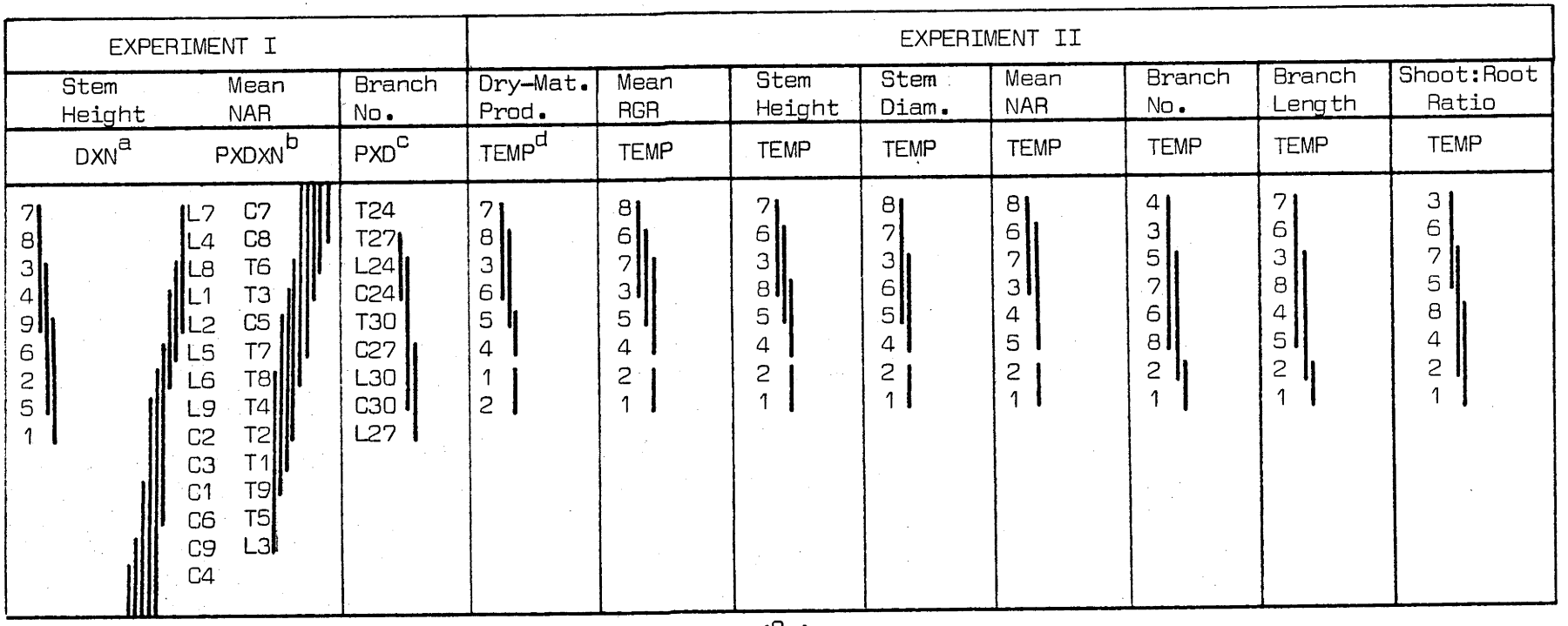
FIGURE 10.1 Multiple Range Test of Means of Growth Parameters of *Pinus caribaea* and *Pinus oocarpa* Seedlings Grown Under Two Ranges of Day x Night Temperatures: High Temperature Range in Experiment I and Low Temperature Range in Experiment II. Relative Values Given.

1. Growth parameters: Means of all growth parameters were calculated from final harvest data of 101 day old seedlings following 132 days of treatment in Experiment I and of 162 day old seedlings following 131 days of treatment in Experiment II. Exceptions were the calculations of mean RGR and NAR (refer Methods).

2. Ranking of means: In descending order from highest at the top to lowest at the bottom.

3. Duncan's multiple range test: Means not connected by vertical line are significantly different at 5% level.

FIGURE 10.1 (Cont'd)



(a) Day x Night temperature: Day/night temperatures (^{o}C) in the high temperature range; (1) 24/18, (2) 24/21, (3) 24/24, (4) 27/18, (5) 27/21, (6) 27/24, (7) 30/18, (8) 30/21, (9) 30/24.

(b) Provenance x Day x Night temperature: P. caribeaea(C); P. oocarpa low (L) and high (T) altitude provenances. Numbers indicate day x night temperatures as in (a).

(c) Provenance x Day temperature: Letters indicate provenances as in (b) and numbers indicate day temperatures in ^{o}C.

(d) Temperature treatment: Day/night temperatures (^{o}C) in the low temperature range (1) 15/10, (2) 18/10, (3) 18/18, (4) 21/10, (5) 21/15, (6) 21/18, (7) 24/18, (8) 24/21.

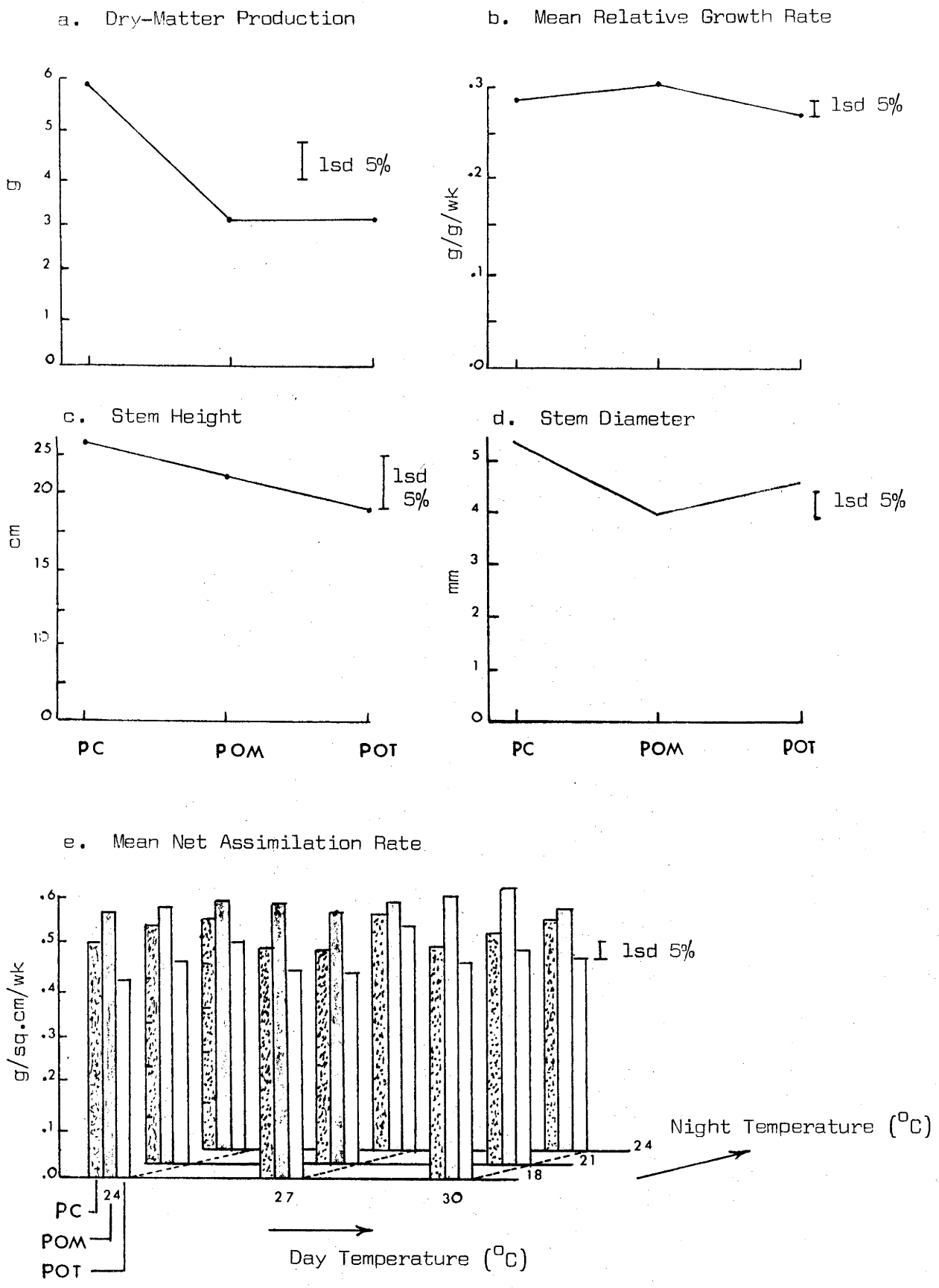


FIGURE 10.2 Growth Response of Seedlings of Pinus caribaea var hondurensis and P. oocarpa var ochoterenai to Varying Day and Night Temperatures. I. High Temperature Range (Day/Night Temperature (°C): 24/18–30/24). P. caribaea (PC); P. oocarpa – Middle (POM) and High (POT) Altitude Sources.

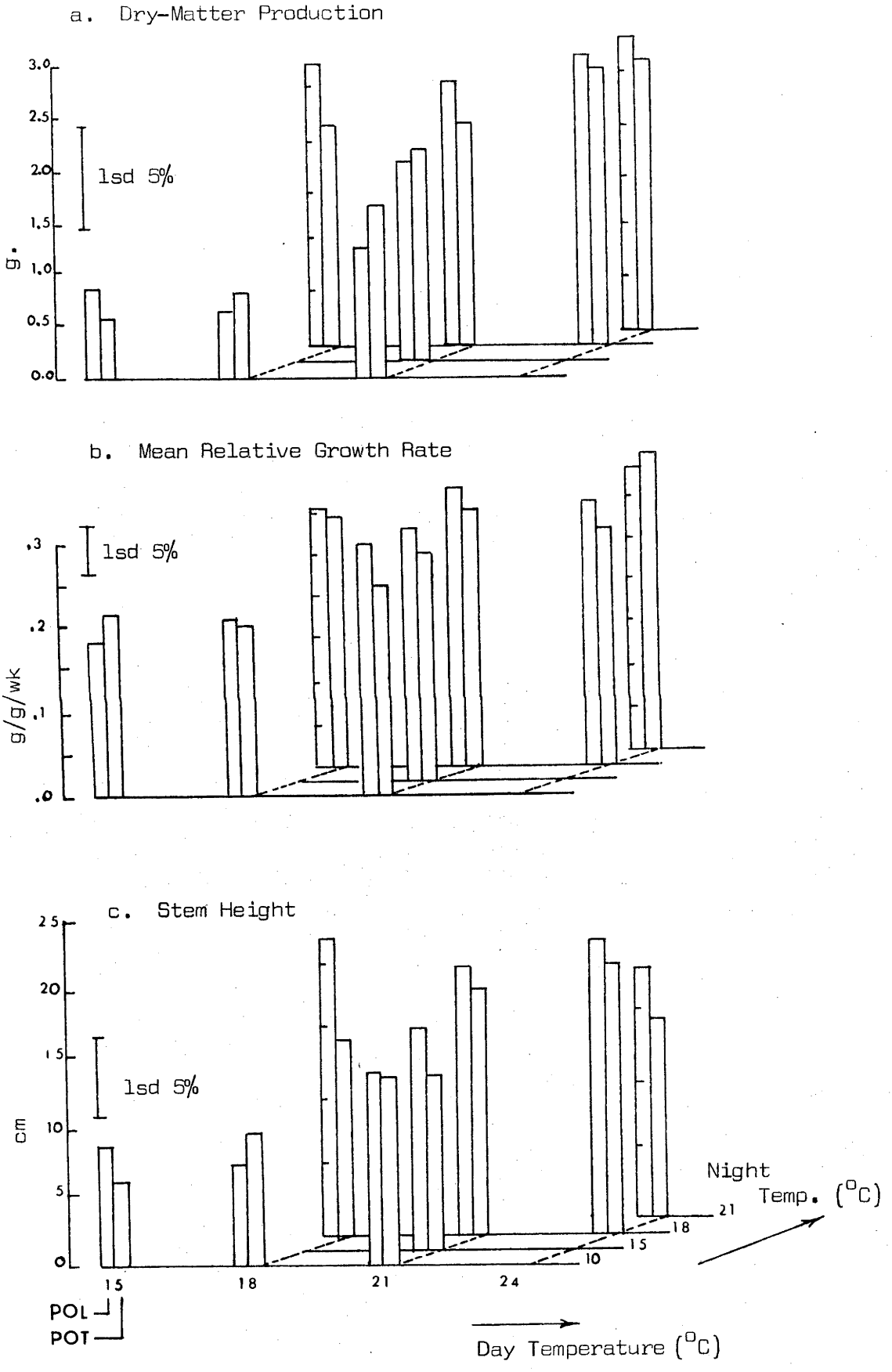
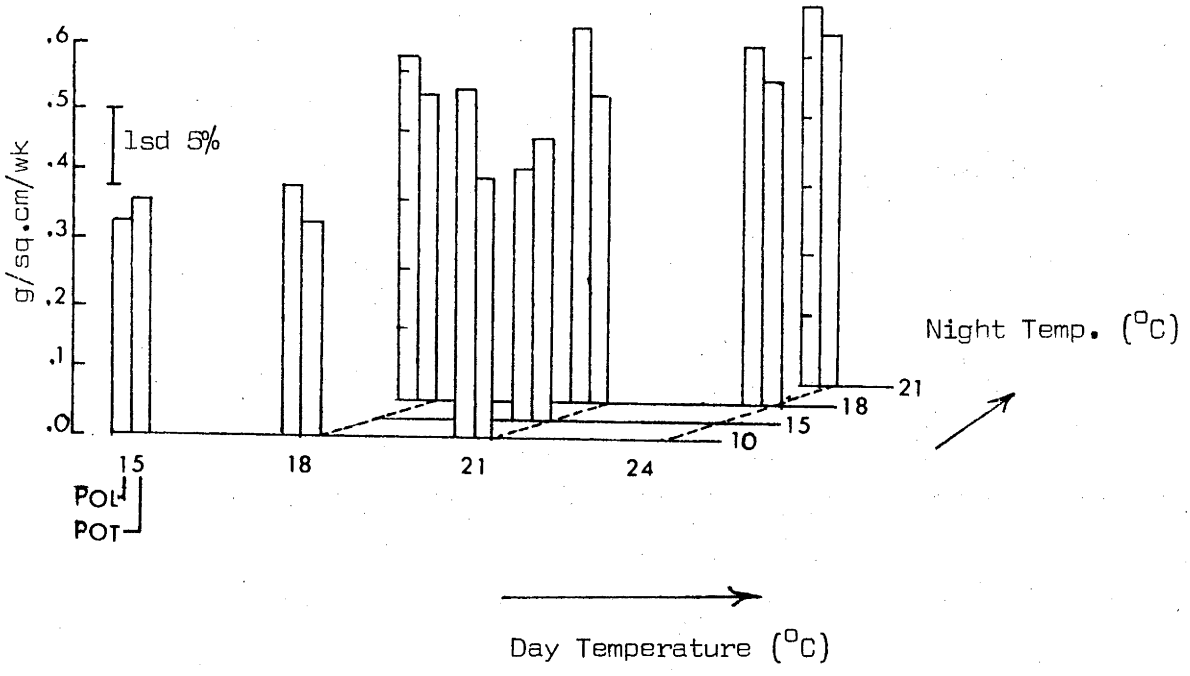


FIGURE 10.3 Growth Response of Seedlings of Pinus oocarpa var ochoterenai to Varying Temperatures: II. Low Temperature Range (Day/Night Temperature (°C): 15/10-24/18). P. oocarpa - Low (POL) and High (PO)

d. Mean Net Assimilation Rate



Height Growth

Inter and intraspecies trends in height growth resembled closely the trends in dry-matter production but with more definite (i.e. significant) differences. In the high temperature range, PC was significantly tallest, POM intermediate and POT significantly shortest (Figure 10.2c). In the lower temperature range, a decrease in height growth with altitude was significant (Figure 10.3c).

Diameter Growth

PC seedlings had the biggest diameter growth in the higher temperature range. Surprisingly, diameter growth in P. oocarpa increased significantly with elevation in reverse to the usual growth trend (Figure 10.2d). The same trend was maintained in the lower temperature range where POT had greater diameter than POL (Figure 10.1).

(b) Analysis of Productivity

Net Assimilation Rate

Net assimilation rate (NAR) in the higher temperature range, was generally highest in POM and smallest in POT seedlings except at 24/24°C, (Figure 10.2e). Provenance differences were generally greater under cooler than under warmer temperature regimes particularly those with warm night temperature (24°C). The trend of decreasing NAR with elevation was also clear in the lower temperature range where NAR in POL was significantly higher than that of POT (Figure 10.3d).

Leaf Weight Ratio

Leaf weight ratio (measured as % needle weight) was unaffected by temperature variation in the higher temperature range. At lower temperatures, there was a significant increase in LWR with elevation.

Altitudinal variation in growth rate in P. oocarpa was due more to variation in photosynthetic efficiency (NAR) than in the photosynthetic system (LWR). In the high temperature range, POM was generally more efficient than POT and to a lesser extent had a better photosynthetic system. In the lower temperatures however, the higher efficiency in POL relative to POT was greatly offset by a smaller photosynthetic system resulting in only a slight advantage in growth rate over that of POT.

The high growth rate in POM over that of PC was mainly due to a more efficient photosynthesis although the latter had a slightly larger photosynthetic system.

(c) BRANCH GROWTH

In the higher temperatures, branch initiation in PC was generally lowest except at 27°C day temperature where it had slightly more branches than POM (Figure 10.1). An altitudinal cline of increasing branch growth (both in number and length) with elevation was clear in P. oocarpa although the increase in branch number under 27°C day temperature was not significant.

In the lower temperature range, the altitudinal increase in branch growth was significant with POT having the most and longest branches.

(d) SHOOT ROOT RATIO

At higher temperatures, proportionally more dry matter was distributed to root growth in PC than in either oocarpa provenances. In the latter, proportionally more dry matter was distributed to shoot growth at higher elevation at both higher and lower temperatures.

(e) SUMMARY

1. Growth and Productivity:

(i) P. caribaea had better growth than P. oocarpa in the higher temperatures tested (24/18 to 30/27°). However, it had slower growth rate than the middle altitude provenance of P. oocarpa (POM).

(ii) An altitudinal cline of decreasing growth with elevation was generally clear in P. oocarpa in the temperatures tested (15/10 to 30/24°C). An exception occurred in diameter growth which showed a reverse trend.

2. Analysis of Productivity:

(i) The difference in growth rate between P. caribaea (PC) and the middle altitude provenance of P. oocarpa (POM) was mainly due to differences in net assimilation rate. PC was significantly less efficient in photosynthesis than POM.

(ii) Differences in growth rate between P. oocarpa provenances were mainly due to differences in net assimilation rate and to a lesser extent due to differences in leaf weight ratio.

3. Branch Growth:

(i) P. caribaea generally had poorer branch initiation than P. oocarpa in the higher temperature range. This was compensated however by a better branch extension growth.

(ii) Branch growth increased with elevation in P. oocarpa.

4. Shoot Root Ratio:

(i) Proportionally more dry matter was distributed to root in P. caribaea than P. oocarpa in the higher temperatures.

(ii) Proportionally more dry matter was distributed to shoot growth in the high altitude provenance (POT) of P. oocarpa than in the lower provenances (POL and POM).

10.3.2 Temperature Differences

(a) Growth and Productivity

Variations in dry-matter production within the higher temperature range (Experiment I) were generally not significant. PC and POM however tended to be most productive at 24/18°C and POT at 30/24°C (Table 10.2). At lower temperatures (Experiment II) POL and POT seedlings grew well under regimes with night temperatures warmer than 15°C and were most productive at 24/18°C (Figure 10.3a). Dry-matter production was lowest under the two coldest temperatures (15/10 and 18/10°C).

At lower temperatures, productivity appears more sensitive to night than to day temperature variation. The standard partial regression coefficient for night temperature was 0.6414 as against 0.2362 for day temperature. Plant dry weight (W) was highly correlated with day (D) and night (N) temperatures in the regression equation, $W = 0.0761\ D + 0.1445\ N - 1.8203$, with $R = 0.8154$.

Growth Rate

Variation in growth rate in the high temperature range, as in dry-matter production, was not generally significant although seedlings tended to grow fastest at 27/18°C (Table 10.2). In the low temperature range, growth rate did not differ under regimes with night temperatures warmer than 15°C and was highest under the warmest temperature (24/21°C), Figure 10.3b.

Height Growth

At higher temperatures growth was generally unaffected by temperature variation except under cool day (24°C) where seedling height was significantly reduced with the drop in night temperature from 24 to 18°C. Height response at the lower temperatures, as in dry-matter production, was best under 24/18°C although comparable with those under regimes warmer than 21/15°C.

Diameter Growth

The drop in night temperature from 24 to 18°C, in the higher temperature range, significantly reduced diameter growth (Table 10.2). In the low temperature range diameter growth was best under the warmest temperature (24/21°C). A high growth was maintained over a wide temperature range with night temperatures warmer than 10°C.

(b) Net Assimilation Rate

Phytosynthetic efficiency (NAR) in PC, in the high temperature range (Experiment I), was generally unaffected by temperature differences (Figure 10.1) although seedlings tended to be most efficient under cool day temperature (24°C). POM was more efficient under cool-mild nights (18 and 21°C), especially combined with warmer days (27 and 30°C) whilst POT maintained a high efficiency over a wide temperature range particularly under warmer day and night temperatures (30°C day and 24°C night temperatures).

At lower temperatures (Experiment II) there was no significant differences in photosynthetic efficiency under the warmer regimes above 21/15°C (Figure 10.3d). Efficiency was highest under the warmest temperature (24/21°C).

(c) Leaf Weight Ratio

The photosynthetic system as indicated by leaf weight ratio was not significantly effected by variation in temperature in contrast to the photosynthetic efficiency of seedlings.

(d) Branch Growth

Although branch length was not significantly varied in the higher temperatures, branch number showed a significant provenance x day temperature interaction at the 5% level, Figure 10.1. PC showed little variation, in contrast to the oocarpa provenances. POL had the most branches under 27°C day decreasing significantly under cool day temperature (24°C), whilst branch number in POM increased significantly with warmer day temperatures.

(e) Shoot:Root Ratio

Dry-matter distribution between shoot and root was not affected by variation in the higher temperatures (Experiment I). At lower temperatures (Experiment II) however, proportionally more dry matter was distributed to the shoot system under warmer regimes with night temperatures above 10°C. The proportion tend to decrease under warm night temperature (21°C), Figure 10.1.

(f) Summary

1. Growth and Productivity:

Growth and productivity in both P. caribaea and P. oocarpa were generally highest in the warmer temperatures between 24/18 and 30/24°C. Good growth was generally maintained under lower regimes with night temperatures above 15°C.

2. Net Assimilation Rate:

Temperature response in NAR differed significantly between species and provenances at higher temperatures (24/18 - 30/24°C). P. caribaea was relatively unaffected by temperature variation whereas POM appeared more efficient under cooler temperatures and POT under warmer temperatures.

3. Leaf Weight Ratio:

Leaf weight ratio was not significantly affected by temperature variation within the temperature range tested (15/10 to 30/24°C).

4. Branch Growth:

At higher temperatures, branch growth in P. caribaea was relatively unaffected by temperature variation in contrast to that of P. oocarpa provenances. In POM the day temperature for maximum number of branch initiation was higher than that of the POT. Branch extension growth was not affected by temperature variation in this range. Generally, branch growth was not affected by low temperatures except under the coldest regimes where growth was reduced.

5. Shoot:Root Ratio:

Temperature effect on shoot:root ratio was only significant in the lower temperature range where proportionally more dry matter was distributed to shoot system in middle temperatures (21/15 to 24/18^{o}C) than at other temperatures.

10.4 DISCUSSION

Differences in magnitude and trends of various parameters were recorded between the two experiments under the common temperature regimes (24/18^{o} and 24/21^{o}C). For example, branching was much greater in Experiment I. In addition both experiments recorded opposing trends in temperature response in shoot:root ratio and height growth.

In a similar experiment with the Eucalyptus series (Chapter 9) such differences were attributed to variation in natural daylight intensity due to the time lapse between experiments.
The suggestion is also applicable here. Consequently, direct comparison between results of the two experiments should necessarily be tentative.

The study provides two bases for comparison: i.e. inter- and intraspecies. The former comparison is confined to the higher temperature range of Experiment I. It is clear from the experiment that P. caribaea was far the superior in growth performance than P. oocarpa. Since the regimes tested were equivalent to temperatures at lower altitudes the performance of the species probably reflect its natural optimum. Whether the species could maintain its

advantage under colder temperature regimes is conjectural and needs further investigation.

Raciation within P. oocarpa was evident as indicated by the generally significant differences in all growth parameters except dry-matter production. A general clinal trend of growth reduction with altitude was also apparent and mainly in physiological characters such as dry-matter production, assimilation rate and growth rate. Differences in branching however did not show the general clinal pattern. This may indicate geographic raciation.

The existence of intraspecies differentiation in P. oocarpa suggests the potential role of temperature in provenance delimitation. It is apparent from the study that the climatic limits of P. oocarpa, as determined by temperature, are potentially greater than their natural limits. For example, the low provenance seedlings continued to grow under the night temperature of 10°C. Such temperature usually occurs at elevations well above the low altitude source (375m). Similarly, the top provenance seedlings grew best at temperatures usually found at lower altitudes. Whether such temperature extremes are experienced at their natural altitudes cannot be ascertained in view of the fragmentary meteorological data available. For the same reason, further suggestion of the species potential limits cannot be made with reasonable certainty. It can however be suggested that temperature is not a limiting factor within the species natural distribution. The role of fire has been suggested as important in determining the species natural range (Luckhoff, 1964).

In view of the variation in growth performance a choice will have to be made between species and provenance in any plantation programme. In the choice of species, P. caribaea is undoubtedly preferred in view of its greater productivity and relative lack of sensitivity to temperature variations in assimilation rate. The species is probably optimally suited in Malaysia to the zones bordering the Lowland Rain Forest - Lower Montane Rain Forest ecotone with the temperature equivalent of $24/18^{o}$-$21/18^{o}$C.

As a plantation species, P. oocarpa is highly versatile. This is indicated by its ability to maintain a suitably high productivity over a wide temperature range from lowland temperatures (as in Experiment 1) up to the altitudinal equivalent of 15^{o}C night temperature (approximately the level of Mt Pine Ridge in British Honduras - c. 900m; Appendix IV). Both species apparently share common optimum elevations noted earlier.

Raciation within P. oocarpa is clearly evident and may require careful choice of provenance. Since differences in assimilation and growth rates were not significantly reflected in dry-matter production, the choice of provenance may be based on morphological characters of the shoot. The top provenance (POT) exhibited poor height growth and greater branching. Both the low and middle provenances (POL and POM) had better form relative to the top provenance and both had the added advantage of more efficient photosynthesis and greater growth rate which may be important within the ecology of the natural environment.

CHAPTER 11

THE EFFECTS OF DAY AND NIGHT TEMPERATURE ON GROWTH OF SEEDLINGS OF PINUS KESIYA ROYLE EX GORDON

11.1 INTRODUCTION

Pinus kesiya Royle ex Gordon (Syn. *P. khasya* Royle; *P. insularis* Endlicher) occurs in the Philippines on the island of Luzon. It is mainly confined to highland areas, principally on the Central Cordillera mountain range with smaller isolated stands on the Caraballo and Zambales mountains (Figure IVb, Appendix IV). Altitudinally the species ranges from c.450m to 2450m.

Temperature variation within the species range is mainly due to elevation. On the Cordilleras for example, the average annual temperature above 1500m is about 18°C whilst at lower elevations the temperature is as high as 25°C. In contrast, seasonal variation is remarkably small as evident from the temperature data shown for Baguio City on the Cordilleras (Table IVb, Appendix IV).

In this experiment growth performance of seedlings from widely spaced altitudinal sources is compared over a range of temperatures to examine whether intraspecies differences occur in *P. kesiya*. Comparison is also made between disjunct seed sources of equivalent altitude from the Cordillera and Zambales mountains to examine whether intraspecies differentiation has occurred due to geographic isolation.

11.2 MATERIALS AND METHODS

The experiment was conducted at CERES phytotron with seed materials supplied by the Forest Research Institute in Canberra. The seed lot numbers were S9257, S9259, S9260, S9269, S9270.

Five geographical and altitudinal provenances of P. kesiya were used. Three from the Cordillera (Northern) region and two from the Zambales (Southern) region. These were the northern low provenance (NL) from 1440-1500m, northern middle provenance (NM) from 1900m, northern top provenance (NT) from 2100m, southern low provenance (SL) from 600-750m and southern top provenance (ST) from 900-1100m elevation. Details of seed origin are given in Section 8.2 and Table 8.1.

The treatment comprised eleven day and night temperature combinations: Nine combinations of three day (15, 21 and 27^{o}C) and three night (10, 16 and 22^{o}C) temperatures plus 21/28 and 27/28^{o}C giving an extension of the upper two day temperatures with a higher night regime, (Table 8.2). This gave a two factorial design, 5 provenances x 11 treatments, with replicates (Table 8.3). However, in the course of experiment treatment 27/22^{o}C was lost thus altering the design to a 5 x 10 factorial.

In the design of experiment, projected temperature values were used as a guide since little meteorological data was available of the seed source. The actual temperatures used were glasshouse temperatures that closely approximated the projected value. Night temperature was emphasised by giving it an extra level although this resulted in negative thermoperiods. It was however considered important in the species growth and distribution.

For some temperature treatments it was necessary to move plants between glasshouses to meet their day and night temperature requirements. For this purpose, these plants were permanently mounted on mobile trolleys. Details of growth conditions in the glasshouses and routine maintenance of experiment are outlined in Sections 8.3 and 8.8.4.

Seedling materials used in the experiment were established according to the standardised procedures outlined for the Oocarpa series in Section 8.8.2. Variation in germination times between the Kesiya series and this series can be considered negligable. The grading procedure used was as outlined in Section 8.8.3.

The harvesting schedule is shown in Table 11.1. Treatment was commenced at about thirty days following germination and lasted 84 days from 10/7/74 to 2/10/74. Five seedlings per provenance were harvested at the start of treatment. One seedling per provenance per treatment was harvested in subsequent harvests except in the final harvest where three seedlings were harvested per provenance and treatment.

TABLE 11.1 Harvesting Schedule: Temperature Experiment with Kesiya Series

Harvest Schedule	Age (days since Treatment[a])	No. of Replicates[b]	Total No. of Replicates Harvested
1	42	1	50
2	56	1	50
3	70	1	50
4	84	3	150

[a] Treatment was commenced at approximately 30 days following germination

[b] Per provenance per treatment

At each harvest the following parameters were measured - stem height and diameter, the component oven dry weights of needles, branches, stems and roots. From these total plant weight, mean relative growth rate and leaf weight ratio (as % needle weight) were calculated. In the final harvest total number of branches and branch length were also measured and shoot root ratio and leaf weight ratio (as % needle weight) calculated. Measurement and calculation procedures were as outlined in Sections 8.5 and 8.7.

Analysis of variance (type II) was conducted on mean relative growth rate and net assimilation rate and on all final harvest data except component dry weights. In the analysis of the former two parameters, the average values of the final harvest, were used, giving four replicates per provenance and treatment, totalling 200 replicates. The analysis of the final harvest data was conducted on three replicates per provenance per treatment, totalling 150 plants. Mortality was negligible and replaced with spare seedlings whenever occurred.

To separate and evaluate the relative effects of day and night temperature on dry-matter production of the final harvest plants, a multiple regression analysis was also conducted (Section 8.7.2).

11.3 RESULTS

Results of the experiment are given in Table 11.2 and Figures 11.2a-e. A summary of the analysis of variance is given in Table 11.3 and means compared with Duncan's multiple range test shown in Figure 11.1.

11.3.1 Growth and Productivity

There was little provenance variations in dry-matter production (DMP), relative growth rate (RGR), height and diameter growth in the Kesiya series. However, the southern low provenance (SL) had lower values for these parameters, especially DMP and height growth (Figures 11.2a-d). Interestingly, there was little variation between the Cordillera provenances and no evidence of an altitudinal trend. In contrast, an altitudinal cline of increasing growth with elevation was generally clear among Zambales provenances and significant in RGR at temperatures with the cold night regime ($10^{o}C$), Figure 11.1.

The multiple regression analysis shown in Table 11.4 suggests that variation in day temperature was generally more influential on DMP than variation in night temperature. The standard partial regression coefficient for day temperature was 0.4602 as against 0.3295 for night temperature. Notably, the low provenances of both the Cordillera and Zambales subseries (NL and SL) appeared more sensitive to night than to day temperatures in reverse to the trends shown by the upper provenances (NM, NT and ST).

Growth and productivity were generally greater under warmer than under colder temperatures. The parameters however differed in temperature response patterns. DMP was little affected by

TABLE 11.2 Growth Response of Seedlings of *Pinus kesiya* from Five Altitudes to Variation in Day and Night Temperatures

TABLE 11.2 (Cont'd)

Parameter	D/N[a]	15/10	15/16	15/22	21/10	21/16	21/22	21/28	27/10	27/16	27/28	Av.	LSD[c] (5%)
1. Dry-Matter Production (g)	NT[b]	0.4281	0.6909	0.5225	1.0542	2.0559	2.0559	1.1236	0.9125	1.1333	1.3621	1.0421	(1) 0.1804
	NM	0.4909	1.0215	0.4347	1.2206	1.2956	1.3682	1.2614	1.0368	1.1716	1.1348	1.0427	(2) 0.2551
	NL	0.2500	1.0155	1.0061	1.0799	1.1579	1.1294	1.2646	0.5985	1.3236	1.5889	1.0414	(3) 0.5704
	ST	0.5844	1.0700	0.4910	1.6253	1.2757	1.2448	1.5274	1.1229	1.3836	1.2200	1.1645	
	SL	0.2359	0.8992	0.4619	1.2743	1.0703	1.9272	1.5218	0.7119	0.9372	1.2249	0.9259	
	Av.	0.3979	0.9376	0.6032	1.2676	1.1707	1.3440	1.3397	0.8765	1.1898	1.3061		
2. Mean Relative Growth Rate (g/g/wk)	NT	0.2666	0.3298	0.3197	0.2910	0.3352	0.3824	0.3864	0.3357	0.3747	0.3633	0.3385	(1) 0.0153
	NM	0.2684	0.3447	0.3250	0.3071	0.3673	0.3320	0.3597	0.3026	0.3591	0.3168	0.3283	(2) 0.0183
	NL	0.2621	0.3043	0.3887	0.3217	0.3738	0.3437	0.3703	0.3429	0.3728	0.3076	0.3388	(3) 0.0485
	ST	0.2643	0.3301	0.3674	0.3620	0.3530	0.3678	0.3652	0.3529	0.3436	0.3773	0.3483	
	SL	0.2039	0.2971	0.3044	0.2868	0.3080	0.3158	0.3544	0.2759	0.3461	0.3766	0.3070	
	Av.	0.2531	0.3212	0.3410	0.3137	0.3475	0.3483	0.3674	0.3220	0.3592	0.3483		
3. Stem Height (cm)	NT	2.60	5.57	5.83	3.80	5.80	9.87	10.10	7.83	8.07	10.93	7.04	(1) 0.94
	NM	3.63	4.83	5.90	3.57	7.30	9.17	9.83	7.40	8.67	9.33	6.91	(2) 1.34
	NL	2.37	4.80	5.90	4.53	8.03	8.03	9.50	5.70	9.13	13.27	7.13	(3) 2.99
	ST	4.47	6.70	7.47	3.67	7.87	8.70	10.10	8.63	10.73	10.10	7.87	
	SL	7.33	4.83	6.57	3.57	6.83	7.40	10.37	6.40	8.17	8.77	6.71	
	Av.	2.98	5.35	6.33	3.83	7.17	8.63	10.41	7.19	8.95	10.48		
4. Stem Diameter (mm)	NT	1.57	1.93	2.50	1.79	2.53	3.30	2.90	2.67	2.80	2.93	2.49	(1) 0.18
	NM	1.83	2.33	2.33	1.63	2.47	2.93	2.80	2.73	2.80	2.73	2.45	(2) 0.25
	NL	1.33	2.03	2.30	2.23	2.37	2.47	3.13	2.23	2.87	2.93	2.39	(3) 0.56
	ST	1.93	2.23	2.70	1.77	2.50	2.60	3.03	2.47	2.77	2.83	2.48	
	SL	1.27	2.23	2.43	1.60	2.27	2.17	3.07	2.60	2.77	2.80	2.32	
	Av.	1.59	2.15	2.45	1.80	2.43	2.69	2.99	2.54	2.80	2.85		
5. Mean Net Assimilation Rate (g/g/wk)	NT	0.4586	0.5435	0.5240	0.4976	0.5397	0.5957	0.6170	0.5515	0.6160	0.6024	0.5546	(1) 0.0304
	NM	0.4707	0.4710	0.5054	0.5111	0.6000	0.5388	0.5715	0.5376	0.5822	0.5279	0.5415	(2) 0.0429
	NL	0.4730	0.5133	0.6097	0.4325	0.6189	0.5524	0.6805	0.6530	0.5970	0.5004	0.5731	(3) 0.0960
	ST	0.4410	0.5405	0.5859	0.6063	0.5794	0.5991	0.5751	0.5851	0.5607	0.6103	0.5684	
	SL	0.3641	0.4765	0.4890	0.4779	0.4929	0.5054	0.5763	0.4691	0.5729	0.5896	0.5014	
	Av.	0.4415	0.5290	0.5428	0.5251	0.5662	0.5583	0.6041	0.5591	0.5858	0.5661		

TABLE 11.2 (Cont'd)

Parameter	D/N[a]	15/10	15/16	15/22	21/10	21/16	21/22	21/28	27/10	27/16	27/28	Av.	LSD[c] (5%)
6. Leaf Weight Ratio (g/g) Arcsin	NT	0.4971	0.4916	0.4979	0.5027	0.5169	0.5292	0.5153	0.5017	0.5129	0.5126	0.4078	(1) 0.0105
	NM	0.4896	0.4921	0.4966	0.5288	0.4875	0.5050	0.5270	0.4972	0.5303	0.5035	0.5052	(2) 0.0149
	NL	0.4657	0.5090	0.5006	0.5420	0.5038	0.5748	0.5108	0.5224	0.5495	0.5107	0.5129	(3) 0.0333
	ST	0.4861	0.4982	0.4895	0.5347	0.4948	0.5022	0.5201	0.5000	0.5093	0.5031	0.5038	
	SL	0.4704	0.5238	0.4778	0.5188	0.5282	0.5153	0.5094	0.4964	0.5144	0.5356	0.5090	
	Av.	0.4817	0.5029	0.4925	0.5254	0.5062	0.5133	0.5153	0.5035	0.5233	0.5131		
7. Number of Branches	NT	0.0	1.3	1.0	3.6	5.7	7.7	9.3	8.0	7.0	3.7	4.7	(1) 2.0
	NM	0.3	2.3	0.7	4.3	4.7	3.7	11.3	7.3	6.3	5.7	4.7	(2) 2.8
	NL	0.0	1.0	0.7	1.0	4.3	5.3	5.0	8.3	9.3	8.7	4.4	(3) 6.3
	ST	0.3	2.3	2.3	7.0	4.3	5.7	10.3	7.7	11.3	7.3	5.9	
	SL	0.0	4.6	1.3	4.0	8.0	2.7	5.7	6.3	8.0	7.0	4.8	
	Av.	0.1	2.3	1.2	4.0	5.4	5.0	8.3	7.5	8.4	6.5		
8. Length of Branches (cm)	NT	0.00	1.43	0.93	4.43	8.73	21.13	14.33	11.63	8.57	15.67	8.69	(1) 1.49
	NM	0.23	2.47	0.50	8.03	6.57	5.20	18.53	8.73	9.17	12.33	7.21	(2) 2.10
	NL	0.00	0.87	0.53	0.90	5.27	9.30	9.67	11.00	21.97	16.33	7.58	(3) 4.70
	ST	0.30	2.63	0.60	10.40	5.73	8.10	18.27	10.40	25.27	12.33	9.53	
	SL	0.00	7.47	0.73	11.40	10.27	5.80	25.43	9.67	17.20	12.33	10.03	
	Av.	0.11	3.03	0.81	7.05	7.35	9.91	17.25	10.29	16.43	13.80		
9. Shoot:Root Ratio	NT	1.7385	2.2362	1.9299	2.2020	2.5636	3.2721	3.1188	2.5362	2.7357	3.0218	2.5355	(1) 0.2373
	NM	1.7983	1.9661	1.8269	2.6970	2.1147	2.4369	2.9203	2.2701	3.2506	2.7278	2.4009	(2) 0.3355
	NL	1.4764	2.0963	2.0388	3.3604	2.7137	2.7338	2.5907	2.8274	4.0196	3.3135	2.7170	(3) 0.7503
	ST	1.8318	2.3064	1.7637	2.8551	2.2528	2.5938	2.9548	2.6711	3.0320	2.8683	2.4990	
	SL	1.5457	2.5702	1.7302	2.6498	2.8683	2.7308	3.1149	2.3655	2.9660	1.4584	2.5807	
	Av.	1.6482	2.2350	1.8579	2.7529	2.5026	2.7535	2.9399	2.5341	3.2008	3.0114		

(a) Day/Night Temperature Treatments (°C)
(b) Provenance: Cordillera (Northern) Provenances:Low (NL), Middle (NM) and High (NT) Altitude Provenance.
Zambales (Southern Provenances: Low (SL) and High (ST) Altitude Provenance.
(c) LSD at 5% level for (1) Provenance, (2) Temperature Treatment and (3) Prov. x Temp.

TABLE 11.3 Summary of Analysis of Variance (Type II) of Various Growth Parameters of *Pinus kesiya* Seedlings from Five Altitudes Grown Under Ten Day x Night Temperatures. Only Mean Values Given.

1. All analysis was conducted on final harvest data of 114 day old seedlings following 84 days of treatment. Exceptions were the ages of seedlings used in the calculation of mean RGR and NAR (refer Methods).

2. Significance levels: *5%, **1% and *** 0.1%.

TABLE 11.3 (Cont'd)

Growth and Productivity

Source of Variation	DF	Dry-Mat. Prod. (g)	Stem Height (cm)	Stem Diam. (mm)	DF	Mean Relative Growth Rate (g/g/wk)
Provenance (P)	4	0.2137*	584*	0.1579	4	0.0099***
Treatment (T)	9	1.6410***	9,916***	3.1451***	9	0.0214***
Harvest (H)	-	-	-	-	3	0.0009
P x T	36	0.1383	289	0.1401	36	0.0021**
P x H	-	-	-	-	12	0.0008
T x H	-	-	-	-	27	0.0027**
Error	100	0.1245	341	0.1203	108	0.0012

Analysis of Productivity

	DF	Mean Net Assimilation Rate (g/g/wk)	DF	Leaf:Weight Ratio (g/g/)x10^2 Arcsin
Provenance (P)	4	0.0330***	4	3.8809
Treatment (T)	9	0.0394***	9	27.0621***
Harvest (H)	3	0.0029	-	-
P x T	36	0.0062	36	5.0964
P x H	12	0.0044	-	-
T x H	27	0.0073	-	-
Error	108	0.0047	100	4.2354

Branch Growth and Shoot:Root Ratio

	DF	Number of Branches	Branch Length (cm)	Shoot:Root Ratio (g/g)
Provenance (P)	4	9.8767	4,419	0.4040*
Treatment (T)	9	129.1526***	55,786***	3.6863***
P x T	36	8.7211	5,104	0.2499
Error	100	15.3400	8,467	0.2154

TABLE 11.4 Multiple Regression Analysis of Plant Dry Weight of Pinus kesiya Seedlings at 84 Days Following Temperature Treatment and 114 Days After Germination.

Provenance	Day Temp.* (D)	Night Temp.* (N)	R
Cordillera Top (NT)	0.4767	0.3445	0.6208
Cordillera Mid (NM)	1.2782	0.1456	0.6061
Cordillera Low (NL)	0.3695	0.6669	0.7991
Zambales Top (ST)	0.5701	0.0720	0.5835
Zambales Low (SL)	0.4035	0.4207	0.5835
All Provenances	0.4602	0.3295	0.5976

R = Multiple Regression Coefficient W = Dry Weight
(*)= Standard Partial Regression Coefficient

Regression Equations	Number of Seedlings
NT W = 0.0425D + 0.0230N − 0.3179	12
NM W = 0.0379D + 0.0068N + 0.1262	12
NL W = 0.0284D + 0.0361N − 0.1974	12
ST W = 0.0405D + 0.0036N + 0.2491	12
SL W = 0.0316D + 0.0232N − 0.1514	12
All W = 0.367D + 0.0185N − 0.0583	60

FIGURE 11.1 Multiple Range Test of Means of Growth Parameters of *Pinus kesiya* Seedlings from Five Altitudes Grown Under Ten Day x Night Temperature Combinations: Relative Values Given.

1. Growth parameters: Means of all growth parameters were calculated from final harvest data of 114 day old seedlings following 84 days of treatment. Exceptions were the calculations of mean RGR and NAR (refer Methods).

2. Ranking of means: In descending order from highest at the top to smallest at the bottom.

3. Duncan's multiple range test: Means not connected by vertical line or in the case of mean RGR occurring outside paired letters (a-a, b-b, c-c etc. in vertical order) are significantly different at 5% level.

FIGURE 11.1 (Cont'd)

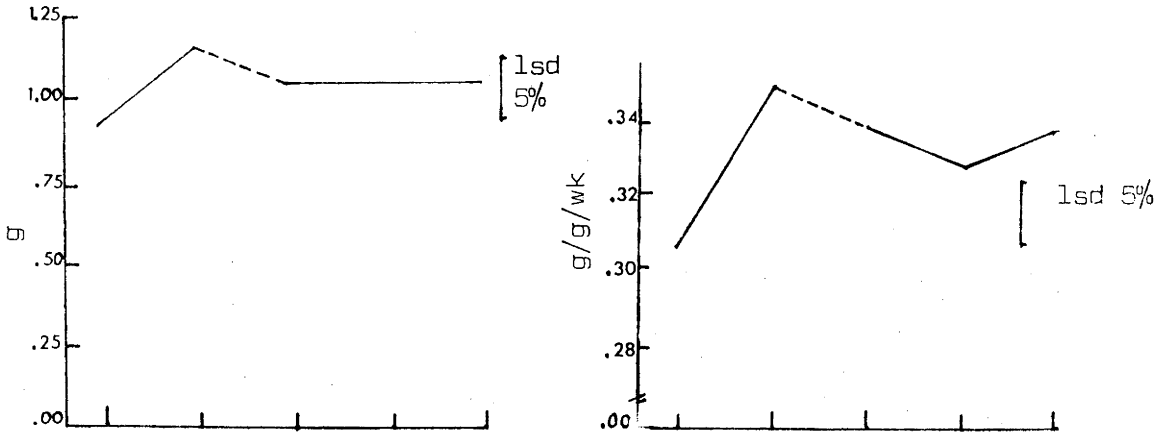
Dry-Mat. Prod.	Mean Relative Growth Rate		Stem Height	Stem Diam.	Mean Net Assimilation Rate	Leaf: Weight Ratio	Number of Branches	Branch Length	Shoot:Root Ratio
T*	P x T**		T	T	T	T	T	T	T
6	NT 3 a	NL8 l	10	7	7	4	9	7	9
7	NL 7 b	NL5	7	10	9	9	7	9	10
10	NL 6 c	NM6	9	9	5	7	8	10	7
4	ST 10d	ST2 m	6	6	10	6	10	8	6
9	SL 10	NL2 a	8	8	8	10	5	6	4
5	NL 9	NM3nb	5	3	6	5	6	5	8
2	NT 5	NT4 c	3	5	3	8	4	4	5
8	NT 9 e	NL3	2	2	2	2	2	2	2
3	NT 7 f	NM10	4	4	4	3	3	3	3
1	ST 6 g	SL6 d	1	1	1	1	1	1	1
	ST 2 h	SL5 e							
	NM 5	ST10f							
	ST 7	NM4							
	NL10	SL3							
	ST 4	NT2 g							
	NM 7 i	NM8 h							
	NM 9	SL2 i							
	SL 7 j	NL4 j							
	ST 5	SL4 k							
	ST 8	SL8 l							
	SL 9 k	NM1 m							
	NM 2	NL1							
	NT 6	ST1 n							
	ST 9	NT1 n							
	NT 8	SL1							

(*) Temperature Treatment: Day/Night temperature (^{o}C) (1) 15/10, (2) 15/16, (3) 15/22, (4) 21/10, (5) 21/16, (6) 21/22, (7) 21/28, (8) 27/10, (9) 27/16 and (10) 21/28.

(**) Provenance x Temperature. Capital letters indicate provenances: Cordillera/ Northern Low (NL), Middle (NM) and Top (NT) altitude provenance and Zambales / Southern Low (SL) and Top (ST) altitude provenance. Numbers indicate temperature treatments as in (*).

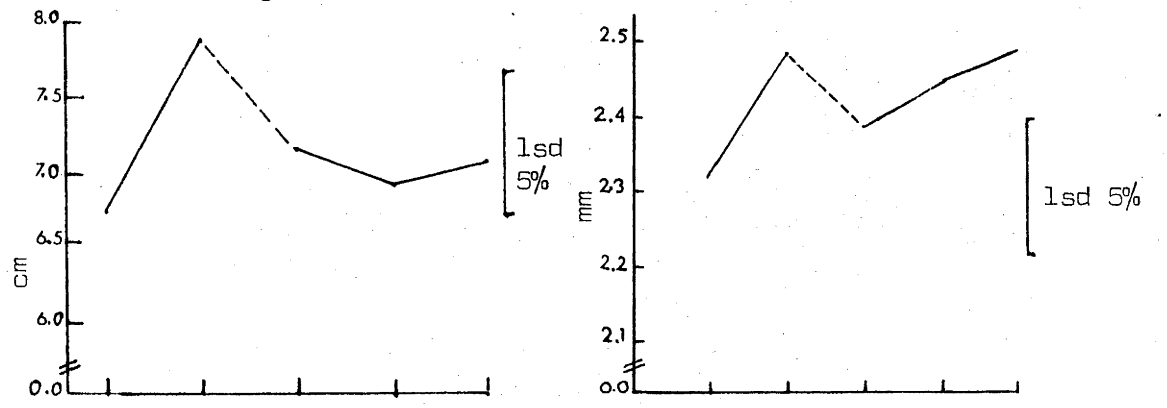
a. Dry-Matter Production

b. Mean Relative Growth Rate



c. Stem Height

d. Stem Diameter



e. Mean Net Assimilation Rate

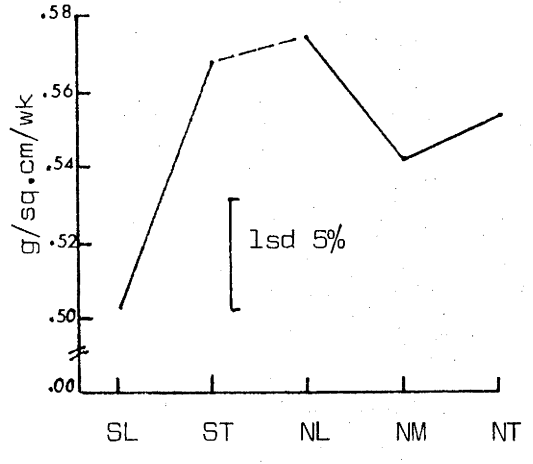


FIGURE 11.2 Growth Response of Seedlings of Pinus kesiya to Varying Day and Night Temperatures. Zambales (Southern) Low (SL) and High (ST) Altitude Provenance. Cordillera (Northern) Low (NL), Middle (NM) and High (NT) Altitude Provenance.

temperature variation in the warm and mild day regimes (21 and 27°C) whilst height growth was highly sensitive to temperature variation (Figure 11.1). Significant provenance x temperature interaction in RGR occurred at the 0.1% level. RGR's in NM and ST were little changed by temperature whilst SL was most responsive to temperature variation.

11.3.2 Analysis of Productivity

There was little variation in net assimilation rate (NAR) and leaf weight ratio (LWR) between provenances except for the significantly low NAR value in the southern low provenance (SL). An altitudinal trend in both NAR and LWR was not evident in the Cordillera provenances whereas a marked trend of increased NAR with altitude was evident in the Zambales provenances (Figure 11.2e).

In the Zambales provenances, significant RGR differences at temperatures with the cold night regime (10°C) were due to variations in both NAR and LWR values. At 27/10°C for example, the higher RGR in ST relative to SL was due to the slightly higher values in both NAR and LWR.

In the warmer regimes at 21/16, 21/22 and 27/28°C, NAR appeared more important than LWR in determining altitudinal trend in RGR. For example, at 21/22°C the lower LWR value in ST relative to SL was offset by a higher NAR which accounted for the slightly higher RGR in ST.

In the Cordillera provenances, NAR was similarly important in determining provenance variation in RGR in the warmer temperature regimes. For example, at the 21/16, 27/16 and 27/28°C regimes,

interprovenance trends in NAR paralelled those for RGR (Table 11.2) in contrast to the trends in LWR. At other regimes however, (e.g., 27/10 and 21/10^{o}C) LWR was also important in determining RGR.

11.3.3 Branch Growth

There was no significant variation in branch number and length between provenances. The Zambales provenances however tended to exhibit better branch growth than the Cordillera provenances (Table 11.2). Branching was generally promoted by warmer temperatures and decreased by colder temperatures as generally evident in the growth and productivity parameters (Figure 11.1).

11.3.4 Shoot:Root Ratio

There was little provenance variation in shoot:root ratio except for the significantly low value in the northern middle provenance (NM). Shoot:root ratio was generally highest in the warmer regimes and lowest in the colder regimes (Figure 11.1).

11.3.5 Summary

1. Growth and Productivity

There was little variation in growth and productivity between provenances except for the generally low growth performance in the southern low provenance (SL). Accordingly, an altitudinal trend is not apparent among the Cordillera provenances (NL, NM, NT) but strongly expressed between the two Zambales provenances (SL and ST).

All provenances generally grew best under warmer temperatures and worst under cooler temperatures. DMP appeared sensitive to

day temperature and was generally high under mild-warm day regimes (21 and 27°C) irrespective of night temperature variation.

2. Analysis of Productivity

In both the Cordillera and Zambales provenances, NAR tended to be important in determining RGR in the warmer temperatures whilst LWR was also important at the cooler temperatures.

3. Branch Growth

Branch growth was little affected by temperature variation between provenances although the Zambales provenances generally tended to exhibit better growth.

4. Shoot:Root Ratio

There was little provenance variation in shoot:root ratio except for the generally significantly low value in the NM provenance.

11.4 DISCUSSION

The origin of seed source appears important in explaining variation in the Cordillera and the Zambales subseries. Seeds of the Cordillera provenances were sampled from within the altitudinal range of optimum growth (1500 - 2200m) generally observed in the field (see Appendix IV). The environmental conditions in this range are typical of the fog-dominated montane environment considered favourable to the growth of P. kesiya (Turnbull, 1971). The lack of altitudinal trend between Cordillera provenances may thus be attributed to the characteristically uniform montane environment.

Seed sources of the Zambales provenances originated from near the altitudinal limits of distribution. The poorer growth performance in SL relative to ST probably indicate its adaptation to environmental conditions marginal to the species as found near the minimum altitudes. Interestingly however, growth performance in ST does not suggest an adaptation to limiting environmental conditions despite its origin from nearer the maximum altitudes of distribution. Its similarity in growth performance to those of the Cordillera provenances could suggest the altitudinal range for optimum growth observed on the Cordilleras may be depressed to lower altitudes on the smaller Zambales mountains due to the Mountain Mass Elevation Effect (see Section 2.2.1).

The similarity in growth performance between ST and the Cordillera provenances is notable in view of their disjunct distribution. It suggests that raciation between geographically disjunct seed sources of equivalent altitude may be absent or weakly expressed despite genetic discontinuity. In contrast, raciation may be more marked between seed sources widely seperated along a common altitudinal transect, as between SL and ST, despite a continuous distribution and probable genetic continuity.

It is clear that temperature is not a limiting factor to the distribution of P. kesiya as apparent from the high productivity maintained under regimes not normally found within the species natural range (e.g., 27/28^{o}C). It is undoubted that fire is important in determining the natural range of the species since the pine forest is basically a fire-subclimax (Kowal, 1966).

Temperature is however probably important in intraspecies distribution of P. kesiya mainly through its effect on RGR. Variation in RGR is clear in the Zambales provenances where the altitudinal trend is marked (Figure 11.1). RGR in the low provenance (SL) was distinctly sensitive to cold temperatures especially those with the cold night regime ($10^{o}C$). This is probably reflected on productivity as suggested by results from the multiple regression analysis (Table 11.3). In contrast, the top provenance (ST) was generally unaffected by temperature variation. This may suggest that SL would be at a competitive disadvantage if it were to co-occur with ST since colder temperatures are more frequent at the upper elevations.

It is probable that temperature may not be important in checking the downward extension of ST in its natural range. Potentially, ST can co-occur with SL at lower elevations since both provenances maintained high RGR under warm temperatures (e.g., $27/28^{o}C$, Figure 11.1). Other environmental factors besides temperature may be limiting to vegetative growth. For example, the occurrance of dessication periods has been reported at lower elevations (Turnbull, 1971).

In the choice of provenance for plantation, the seed sources tested in the experiment are suitable on the basis of DMP except for the less productive SL provenance. If RGR is also included in the criteria, NM and ST are preferred over the others since both can be grown over a wider temperature range without appreciably affecting growth rate (Figure 11.1).

The location of plantation is important since growth and productivity are clearly affected by variations in temperature. For high productivity it is suggested plantations should be located in areas with day regimes warmer than 15°C whilst night temperature can be as low as 10°C. However, to maintain good stem growth (both in height and diameter) plantations should perhaps be sited within a narrower temperature range of between 21-27°C day temperatures and 16-28°C night temperatures.

As noted earlier, temperature may not be important to vegetative growth at the minimum altitudes of distribution although performance in the warmer temperatures is generally high in the experiment. Field studies, complemented with investigations into the role of other environmental factors in controlled experiments, are therefore necessary. For this reason extrapolation of field performance must be conservative.

It is desirable in plantation programmes to select provenanes with higher growth rates. Selection for this trait is generally incorporated in three improvement programmes. In P. kesiya the basis for improvement of growth rate between provenances tested differs between temperatures. The results suggest that at warmer temperatures, selection for a high NAR is probably important in increasing RGR whereas at lower temperatures the selection for both high NAR and LWR are considered important.

CHAPTER 12

EFFECTS OF FROST ON SEEDLINGS OF EUCALYPTUS DECAISNEANA

12.1 INTRODUCTION

The occurrance of frost on tropical highland is generally known (Richards, 1964). Knowledge of its influence on the flora of these areas is however lacking. It has been suggested by Holdridge et.al., (1971) that floristic composition is markedly changed across the frost line (Section 3.5.1, Figure 3.2). Whether frost effect is discernable at the intraspecies level is generally unknown.

E. decaisneana is an example of a tropical broad leaved species whose distribution transverses the frost line. Occasional frost is recorded at the uppermost seed source, ET, while no frost occur at the altitudes of the lower seed sources (Turnbull, pers. comm.). Studies on clinal populations of temperate Eucalypts have been reported (Pryor, 1957; Ashton, 1958; Boden, 1958). Similar studies on tropical Eucalypts have not been conducted to date. In the following experiment the probability of intra-species differences in frost effect on E. decaisneana is examined.

12.2 MATERIALS AND METHODS

Four week old seedlings, established under the standard establishment procedure detailed in Section 8.8.2 were conditioned for frost studies at 15/10^{o}C day and night temperature from twelve to

seventeen weeks (from 16/8/74 to 11/12/74) between frost runs (Table 12.1). A conditioning period was considered necessary since tropical species are generally frost sensitive. There were only a limited number (about 135) of seedlings available for frost treatment. As the response to any one treatment could not be anticipated the available plants were divided into three separate groups for seperate frost treatments. This gave fourteen plants per treatment per provenance, of which four were selected at random and used as untreated controls.

Frost treatment facilities available at CERES phytotron have been described by Morse and Evans (1962). Frost temperature was maintained within an accuracy of $\pm 0.5^{o}C$ by a thermostat device. The latter adjusts temperature drifts within cycles of 10 minutes and a continuous temperature record is kept on a running chart. Light was switched off during frost run and wind speed was kept minimal. Prior to each treatment a dummy run was made to test accuracy of the frost temperature.

Cell water content is important in influencing frost injury (Mazur, 1969). To minimise differences, seedlings were watered approximately one hour before treatment and free surface moisture dried. In addition, to minimise further moisture loss through transpiration seedlings were kept under condition of high humidity until treatment commenced.

For frost runs, seedlings were closely packed, in a random arrangement, in two frost boxes (84cm x 69cm x 37cm) and buried up to the level of root collar in dry perlite to protect roots from frost damage. Spaces were allowed between seedlings and box walls for free air circulation.

The boxes were placed centrally, with intervening space, in the frost room at about fifteen minutes before treatment to allow the temperature to stabilise. At the end of treatment the cooling device was automatically switched off and temperature allowed to drift upwards to a stable level. Seedlings were then removed back to the 15/10°C glasshouse and immediately watered. Normal watering and nutrient regime were continued throughout the recovery period.

Details of the frost treatments are shown in Table 12.1. The period of recovery, twelve days, was determined visually in the first run and maintained in subsequent runs. Visual estimates of frost injury in the first run prompted the reduction of treatment duration from twelve to six hours for the second run. The treatment was repeated in the third frost run.

TABLE 12.1 Frost Treatments: Eucalyptus Series

Run No.	Treatment	Time/date of Frost Run		Age since germination (weeks)	Conditioning period under 15/10°C (weeks)
1	-1°/12hrs	2100hrs	7/11/74	16	12
2	-1°/ 6hrs	2100hrs	14/11/74	17	13
3	-1°/ 6hrs	2130hrs	11/12/74	21	17

Frost injury was measured in terms of the percentage ratio of dry weight:fresh weight of leaves (R) at the end of the recovery period (after Paton, 1972). Later studies have shown R to be a reliable index of frost injury (for example, Awe and Shepherd, 1975). R was calculated according to the formula;

$$R = \frac{\text{Dry weight of leaves}}{\text{Fresh weight of leaves}} \times 100$$

The magnitude of R may be affected by moisture status of leaves during weighing and by dry matter increment following recovery. Moisture status in harvested leaves is particularly important since differences in fresh weight of leaves affect value of R especially when injuries are severe. To avoid moisture stress developing during harvest, seedlings were watered, drained and kept in the $15/10^{o}C$ glasshouse where Relative Humidity at night exceeds ninety percent. Seedlings were taken out individually, leaves stripped and carefully dried before weighing. Leaves shed following treatment were also included in the weighing.

Normal dry matter increment is resumed following the critical recovery period beyond which R is increasingly distorted (Paton, 1972). Because of the shortage of seedlings quantitative determination of the recovery period was not attempted. It was assumed differences in increment of dry matter were small in the cold ambient temperature ($15^{o}/10^{o}C$) in which seedlings were kept.

Untreated control plants were first analysed for intra-species differences in R values before the actual analysis of treated plants. Whether such differences occur in untreated provenances was not apparent from previous studies.

12.3 METHOD OF ANALYSIS AND RESULTS

R values for the untreated control plants varied between 24 and 34%. A standard value for untreated control plants was defined therefore as 30% and the final adjusted frost injury figures were calculated:

$$\text{Adjusted Frost Injury, } R' = \frac{R}{R_c} \times 30$$

where, R_c is the mean R value of the control plant for the particular treatment.

Analysis of variance of the transformed (arcsin) R values of the control plants alone (Table 12.2) showed significant provenance ($p > 0.1\%$) and provenance x treatment differences ($p > 5\%$). Accordingly a common R_c value could not be used for all seedlings. A mean R_c value was calculated from the four control seedlings within each provenance and treatment and this R_c value used to calculate the Adjusted Frost Injury for the corresponding treated seedlings of the same provenance in the same treatment.

To demonstrate the importance of adjusting the R value to accord with the controls, where intra-species differences do exist between the controls, adjusted and non-adjusted R values were analysed and compared. Table 12.3 summarizes the analysis of variance results for both R values. The means of R' values are shown in Table 12.4.

There is clearly a considerable difference between adjusted and non-adjusted values of R (Table 12.3). Differences between treatments are significant ($p > 0.1\%$) in both values. But provenance

TABLE 12.2 Analysis of Variance of R Values in Untreated Control Plants: Eucalyptus Series

Source	DF	Mean Square	'F'
1. Provenance	2	52.8164	***
2. Treatment	2	3.0947	
3. Prov. x Treatment	4	11.6428	*
4. Error	27		
Total	35		

Significance level: *5%, ***0.1%.

TABLE 12.3 Analysis of Variance of Treated Plants for Adjusted and Unadjusted R Values: Eucalyptus Series

Source	DF	Unadjusted R	Adjusted R
		Mean Square	Mean Square
1. Provenance	2	185.0674	1446.1104***
2. Treatment	2	1012.3262***	1813.4121***
3. Prov. x Treatment	4	32.3149	421.4731**
4. Error	81	83.66	94.3516
Total	89		

Significance Level: *5%, **1%, and ***0.1%.

TABLE 12.4 Means of Adjusted R Values (%) of Treated Plants: Eucalyptus Series

Provenance	Treatment 1	Treatment 2	Treatment 3	Prov. $\bar{R}$
	$-1^{o}C$/12hrs	$-1^{o}C$/6hrs	$-1^{o}C$/6hrs	
Low (L)	71.1	51.3	54.8	59.2
Middle (M)	94.6	63.9	59.5	75.1
Top (T)	58.0	43.9	56.5	52.8
Treatment $\bar{R}$	76.8	53.1	57.0	

Duncan's Multiple Range Test

Means not connected by a horizontal line are significantly different at 5% level. L,M and T are Low, Middle and Top altitude provenances respectively. Numbers indicate frost treatment.

M1 L1 M2 M3 T1 T3 L3 L2 T2

---

differences and provenance x treatment interaction are significant in R' (respectively $p > 0.1\%$ and $p > 1\%$) but not in R.

Comparison of provenance x treatment means (R' values) using Duncan's Multiple Range test (Table 12.4) showed provenance differences were greatest in the first treatment where frost exposure was 12 hour s (Table 12.1). In this treatment frost injury was significantly more severe in the seedlings of the middle altitude provenance (R = 94.6%) than in the seedlings of the other provenances. Seedlings of the top provenance were least injured (R' = 58.0%) but did not differ significantly from seedlings of the low provenance (R' = 71.7%).

In subsequent treatments provenance differences were less distinct. Frost injury was always greatest in seedlings of the middle altitude provenance (Table 12.4). The difference was especially apparent in the second treatment where significant differences in frost injury occurred between seedlings of the middle and top provenances.

It also appears with the material used in the experiment that R is independent of seedling size as suggested by Paton (1972). Seedlings between the second and third frost run differed in age and size but not in frost treatment (Tables 12.1, 12.4). Nevertheless, the difference in frost injury between the two treatments in all provenances was not significant. Similarly, there was no significant difference in R values of control plants between frost runs in spite of the differences in size due to the lapse of five weeks between the first and third run (Tables 12.1, 12.2).

12.4 DISCUSSION

Within species differences in frost resistence occur in Eucalyptus decaisneana. Seedlings from the middle altitude provenance tended to be more susceptible to frost injury than seedlings from the upper or lower altitude seed sources. Interestingly, seedlings from the highest provenance, while being the most frost resistant, do not differ from low provenance seedlings under the frost conditions tested.

It appears that the factor or factors responsible for frost tolerance are not necessarily correlated with altitude. Conditions inducing frost tolerance within the population appear relatively ineffective in the middle altitudes but not in the upper and lower altitudes.

This agrees with the results of similar studies on Eucalyptus species. Studies on Eucalyptus viminalis also showed lower and higher altitude seed sources were more frost resistant than a middle altitude source (Paton, 1972). A clinal pattern was however evident above a certain critical altitude. Such a pattern may be apparent in Eucalyptus decaisneana if a greater number of samplings from the upper altitudes of distribution were tested.

The choice of provenance within species which differ in frost resistance may be important above the frost line. In the establishment of plantations near or above the frost line the choice for frost tolerance should be considered.

CHAPTER 13

THE EFFECTS OF LIGHT INTENSITY ON THE GROWTH OF EUCALYPTUS DECAISNEANA SEEDLINGS

13.1 INTRODUCTION

Light intensity reaching the seedling layer of tropical highland stands vary greatly between altitudinal vegetation zones. The major factor regulating zonal light intensity is fog which markedly reduces light intensity (see Table 3.3, Section 3.4.1) and generally exerts a dampening influence on its annual variation pattern (Brown, 1919). Thus, in the montane zones where fog is frequent, light intensity is lower than that in the lowlands (Beard, 1946).

Zonal variation in stand structure, specifically variation in the amount of upper canopy foliage, further modify light intensity at the seedling level. The more compact canopy foliage of the Lowland Rain Forest and Lower Montane Rain Forest stands cuts off more light reaching the floor than the relatively more open canopy of the Upper Montane Rain Forest stand (Grubb and Whitmore, 1966; Baynton, 1968).

It is possible that E. decaisneana seedlings are conditioned to differences in light intensity within its natural range since variation in both fog frequency and stand structure occurs between altitudes (Appendix IV). Whether this conditioning is strong enough to cause intraspecies differences in growth response to different levels of light intensity is examined in this experiment.

13.2 MATERIALS AND METHODS

The experiment was conducted at CERES phytotron with seed sources supplied by the Forest Research Institute in Canberra (seed lot numbers; s10135, s10136 and s9016).

Seed sources of the Eucalyptus series were used; namely, the low provenance (EL) from 570m, the middle provenance (EM) from 1554m and the high provenance (ET) from 2743m elevation. For detailed origin of the seed sources refer Section 8.2 and Table 8.1.

The treatment comprised three shade intensities determined by the available materials with one control (no shade) - namely, 15%, 51%, 62% and 100% of full light intensity - in a two factorial, 3 provenances x 4 treatments design (with replicates).

Shade was provided by green 'sarlon' shade cloth available over a range of shade intensities. The selection of shade cloth used was based on preliminary measurements of relative light intensity under shade with a photometer. For the shade intensities of 15% and 51% more than one layer of shade cloth were used.

The following formula was used:

$$\text{Relative light intensity} = \frac{\text{Light intensity under shade}}{\text{Light intensity in daylight}} \times 100\%$$

To minimise variation in reading the following precautions were observed: (1) all measurements were made only under clear sky condition around 1200 hours, (2) only maximum readings were taken; (3) each reading was taken at exactly 30cm beneath the shade cloth; and (4) readings were replicated.

The shade cloth was mounted over a wire frame work measuring 100cm (length) x 88cm (breadth) x 88cm (height). All sides were carefully covered except for the floor. There was no danger of light entering from this source since all frames were mounted on ventilation pumps. Access to plants was provided through a flap in the front of the structure. All cut edges were sewn into the framework thus effectively covering the edges.

All shade frames were located in the same glasshouse with 27/22^{o}C day and night temperature regime. They were carefully spaced to avoid all neighbouring shades. Control plants were also located in the same glasshouse. Free air circulation from the ventilation pumps beneath the shade frames and control plants ensured no temperature differences from that of the glasshouse.

Shade intensities in the frames were again measured under similar precuations related above. Five readings were taken at plant height (about 30cm below the roof), one from each corner and one in the centre.

Growth conditions and routine maintenance in the glasshouse are outlined in Sections 8.3 and 8.8.4.

Seedling materials used were established and graded according to the standardised procedures outlined in Sections 8.8.2 and 8.8.3.

The harvest schedule is shown in Table 13.1. Treatment was started approximately 30 days following germination and lasted 42 days from 31/10/74 to 12/12/74. Twelve seedlings were harvested per provenance in the initial harvest. Two seedlings per provenance and treatment were harvested in the first five harvests and twelve in the final harvest.

TABLE 13.1 Harvest Schedule : Light Experiment with Eucalyptus Series

Harvest Schedule	Age (days) since treatment[a]	No. of Replicates[b]	Total No. of Replicates harvested
1	15	2	24
2	21	2	24
3	28	2	24
4	35	2	24
5	42	12	144

[a] Treatment commenced at approximately 30 days after germination.

[b] Per provenance and per treatment

At each harvest height and diameter, leaf area and component oven dry weights - leaves, branches, stems and roots - were measured and mean relative growth rate and net assimilation rate and plant weight calculated. In the final harvest the following additional parameters were measured or calculated - branch number and length, number of leaves, leaf length and breadth of sample leaves (fully expanded leaves between the seventh and eleventh nodes generally), specific leaf area, shoot root ratio and leaf weight ratio (as % leaf weight). Measurement and calculation procedures were as outlined in Sections 8.5 and 8.7.

Analysis of variance (type II) was conducted on all final harvest results except the component dry weights. Since there were sufficient replicates in the final harvest only growth rate and assimilation rate data of this harvest were analysed. In total there were 144 replicates in the final harvest. There was no missing values since there was sufficient space to carry four to five spare plants throughout the experiment.

13.3 RESULTS

Detailed results of the experiment are given in Table 13.2, and the analysis of variance summarized in Table 13.3. Means of parameters with significant interaction were ranked and compared using Duncan's multiple range test in Figure 13.1.

It should be noted that light treatments used were defined in relative values taking full sunlight as 100%.

13.3.1 Growth and Productivity

Growth and productivity decreased with shading being highest under low shade (62% - 100%) and lowest under heaviest shade (15%). The most outstanding feature was the similarity in growth response of the lower provenances (EL and EM) in contrast to that of the top provenance (ET).

The response patterns for the lower provenances (EL and EM) were generally similar for dry-matter production, relative growth rate, height and diameter values (Figures 13.1-1). These factors were not significantly affected by low shade (62% - 100%). With further shade (62%), growth was generally and significantly reduced except for height which exhibited a slightly greater shade tolerance (Figure 13.2c). In EL, although there was no significant difference compared to EM, dry-matter production and height growth were slightly better at light shade (62%) than under full light.

The optimum light intensity for growth in EL and EM probably lie between 62% and full light intensity with the possible exception of height growth in EL which was probably higher (51% - 62%),

TABLE 13.2 Growth Response in Seedlings of *E. decaisneana* from Three Altitudes Grown Under Four Relative Light Intensities

Except for Maan Relative Growth Rate and Mean Net Assimilation Rate all values were determined from final harvest data of 72 day old seedlings following 42 days under treatment.

TABLE 13.2 (Cont'd)

Parameter		Relative Light Intensity (Full Daylight = 100%)				Average	L.S.D.[b] (5%)
		16%	51%	62%	100%		
1. Dry Matter Production (g)	ET[a]	0.3041	1.0216	1.6312	2.2841	1.3105	(1) 0.2799
	EM	1.0145	3.1786	4.2425	4.2621	3.1744	(2) 0.3232
	EL	0.7302	2.6718	4.6303	4.2512	3.0709	(3) 0.5598
	Av.	0.6829	2.2907	3.5016	3.5991		
2. Mean Relative Growth Rate (g/g/wk)	ET	0.1993	0.4022	0.4816	0.5392	0.4056	(1) 0.0318
	EM	0.3969	0.5984	0.6461	0.6494	0.5727	(2) 0.0367
	EL	0.3479	0.5656	0.6602	0.6466	0.5551	(3) 0.0635
	Av.	0.3147	0.5221	0.5960	0.6118		
3. Stem Height (cm)	ET	9.9	20.0	24.2	26.3	20.1	(1) 0.21
	EM	27.0	46.0	44.5	44.1	40.4	(2) 0.24
	EL	25.9	46.7	48.3	40.3	40.3	(3) 0.42
	Av.	20.9	37.5	39.0	36.9		
4. Stem Diameter (mm)	ET	1.77	3.01	3.83	4.10	3.18	(1) 0.196
	EM	2.65	4.18	4.61	4.57	4.00	(2) 0.226
	EL	2.34	3.86	4.73	4.57	3.87	(3) 0.392
	Av.	2.25	3.68	4.39	4.41		
5. Mean Net Assimilation Rate (g/sqcm/wk.)	ET	0.0009	0.0020	0.0027	0.0033	0.0022	(1) 0.00028
	EM	0.0016	0.0034	0.0040	0.0046	0.0034	(2) 0.00032
	EL	0.0013	0.0028	0.0041	0.0043	0.0031	(3) 0.00055
	Av.	0.0013	0.0027	0.0037	0.0041		
6. Leaf Area Ratio (sq cm/g)	ET	264.15	241.85	221.23	207.93	233.79	(1) 6.275
	EM	264.68	198.13	186.54	171.72	205.27	(2) 7.246
	EL	301.87	229.76	199.26	191.12	230.50	(3) 12.550
	Av.	276.90	223.25	202.34	190.26		
7. Specific Leaf Area (Sq cm/g)	ET	487.01	429.03	381.17	337.00	408.55	(1) 24.316
	EM	606.58	394.35	354.76	290.99	411.67	(2) 28.078
	EL	672.36	465.73	349.73	310.02	449.46	(3) 48.633
	Av.	588.65	429.70	361.89	312.67		

TABLE 13.2 (Cont'd)

Parameter		Relative Light Intensity (Full Daylight = 100%)				Average	L.S.D.[b] (5%)
		18%	51%	62%	100%		
8. Leaf Weight Ratio (g/g) x 10^2 Arcsin Values	ET	50.26	48.73	46.70	46.17	47.97	(1) 1.000
	EM	47.05	44.45	43.77	43.98	44.81	(2) 1.155
	EL	48.52	44.95	43.99	44.52	45.50	(3) 2.000
	Av.	48.61	46.04	44.82	44.89		
9. Total Leaf Area (sq cm)	ET	87.45	240.45	318.67	388.94	258.88	(1) 45.332
	EM	308.24	605.09	722.12	591.43	556.72	(2) 52.345
	EL	265.95	595.33	770.56	635.78	566.90	(3) 90.664
	Av.	220.55	480.29	603.78	538.72		
10. Total Leaf Number	ET	25	36	46	61	42	(1) 9.0
	EM	45	74	96	103	80	(2) 10.4
	EL	31	78	104	88	75	(3) 18.0
	Av.	34	63	82	84		
11. Leaf Length (mm)	ET	60.7	83.1	91.8	86.2	80.5	(1) 5.13
	EM	86.2	100.8	107.4	88.7	95.8	(2) 5.93
	EL	91.0	107.0	109.0	108.6	103.9	(3) 10.27
	Av.	79.3	97.0	102.7	94.5		
12. Leaf Breadth (mm)	ET	26.7	39.5	44.7	42.4	38.4	(1) 3.56
	EM	43.9	53.1	55.7	47.8	50.1	(2) 4.11
	EL	50.0	61.9	64.5	60.8	59.3	(3) 7.12
	Av.	40.2	51.5	55.0	50.4		
13. Leaf Length/Breadth (mm/mm)	ET	2.27	2.13	2.11	2.07	2.14	(1) 0.069
	EM	1.99	1.90	1.94	1.88	1.93	(2) 0.079
	EL	1.83	1.83	1.77	1.81	1.81	(3) 0.138
	Av.	2.03	1.95	1.94	1.92		
14. Number of Branches	ET	1.3	2.4	3.8	6.0	3.4	(1) 1.36
	EM	4.8	9.5	10.9	12.8	9.5	(2) 1.57
	EL	1.3	9.9	13.4	11.0	8.9	(3) 2.73
	Av.	2.5	7.3	9.4	9.9		
15. Branch Length, cumulative (cm)	ET	3.9	19.7	23.8	53.2	25.2	(1) 16.6
	EM	26.8	90.7	116.7	137.7	93.0	(2) 18.0
	ET	6.9	85.9	145.6	117.5	89.0	(3) 31.1
	Av.	12.5	65.4	95.4	1 02.8		

TABLE 13.2 (Cont'd)

Parameter		Relative Light Intensity (Full Daylight = 100%)				Average	L.S.D.[b] (5%)
		18%	51%	62%	100%		
16. Shoot:Root Ratio (g/g)	ET	3.89	4.96	4.17	4.47	4.37	(1) 0.260
	EM	5.76	5.30	5.06	5.34	5.36	(2) 0.300
	EL	4.80	5.87	5.15	4.52	5.08	(3) 0.517
	Av.	4.82	5.38	4.80	4.78		

(a) Provenances or altitudes: Low altitude provenance (EL) from 570m; Middle altitude provenance (EM), 1554m; Top or high altitude provenance (ET) from 2743m.

(b) L.S.D. values of 5% level are given for (1) provenance, (2) treatment and (3) provenance x treatment.

TABLE 13.3 Summary of Analysis of Variance (Type II) of Various Growth Parameters of Eucalyptus decaisneana Seedlings from Three Altitudes Grown Under Four Relative Light Intensities. Only Mean Square Values Given.

1. With the exception of mean RGR and NAR, analysis was conducted on harvest data of 72 day old seedlings following 42 days of treatment.

2. Significance levels: *5%, **1% and *** 0.1%.

TABLE 13.3 (Cont'd)

Growth and Productivity

Source of Variation	D.F.	Dry-Matter Production (g)	Mean Relative Growth Rate (g/g/wk)	Stem Height (cm)	Stem Diameter (mm)
Provenance (P)	2	52.6723***	0.4048***	6564.50***	9.55***
Treatment (T)	3	66.6673***	0.6725***	2589.50***	36.93***
P x T	6	3.8662***	0.0068	128.46***	0.36
Error	132	0.4894	0.0063	28.09	0.24

Analysis of Productivity and Analaysis of Photosynthetic System

	D.F.	Mean Net Assimilation Rate ($g/cm^2/wk$) x 10^{-4}	Leaf Area Ratio (cm^2/g) x 10^{-2}	Specific Leaf Area (cm^2/g)	Leaf Weight Ratio (Arcsin)
Provenance (P)	2	0.1918***	1.1693***	24,899***	132.3105***
Treatment (T)	3	0.5484***	5.2850***	520,714***	112.9128***
P x T	6	0.0076	0.2558***	35,395***	4.0163
Error	132	0.0048	0.0246	3,694	6.2482

Leaf Parameters

	DF	Total Leaf Area (cm^2)	Total No. of Leaves	DF	Leaf Length (mm)	Leaf Breadth (mm)	Leaf Length: Breadth (mm/mm)
Provenance (P)	2	1,469,580 ***	20,208 ***	2	14,174 ***	11,019 ***	2.8310 ***
Treatment (T)	3	1,015,410 ***	19,586 ***	3	7,493 ***	3,030 ***	0.1766*
P x T	6	53,220 ***	16,62 ***	6	773*	157	0.0445
Error	132	12,838	507	288	343	165	0.0615

TABLE 13.3 (Cont'd)

Branch Growth and Shoot:Root Ratio

	DF	Number of Branches	Branch Length (cm)	Shoot:Root Ratio (g/g)
Provenance (P)	2	549.1***	69,511.70***	12.4882***
Treatment (T)	3	414.5***	60,479.51***	3.0369*
P x T	6	55.5***	7,734.13***	2.2846*
Error	132	11.6	1,511.46	0.8777

FIGURE 13.1 Multiple Range Test of Means of Growth Parameters of *E. decaisneana* Seedlings from Three Altitudes Grown Under Four Relative Light Intensities. Relative Values Given.

1. Values not connected by horizontal line are significantly different at 5% level under Duncan's multiple range test.

2. Altitudes or provenances (PROV): Low (L) 570m; Middle (M) 1554m; Top (T) 2743m altitude.

3. Relative light intensities (TMT) (taking full daylight as 100%): (1) 100%; (2) 62%; (3) 51%; (4) 16%.

FIGURE 13.1 (Cont'd)

Increasing Value ←

1. Dry-Matter Production	PROV:	L	M	L	M	M	L	T	T	T	M	L	T
	TMT:	2	1	1	2	3	3	1	2	3	4	4	4
2. Stem Height	PROV:	L	M	L	M	M	L	T	T	T	M	L	T
	TMT:	2	1	1	2	3	3	1	2	3	4	4	4
3. Leaf Area Ratio	PROV:	L	M	T	T	L	T	T	L	M	L	M	M
	TMT:	4	4	4	3	3	2	1	2	3	1	2	1
4. Specific Leaf Area	PROV:	L	M	T	L	T	M	T	M	L	T	L	M
	TMT:	4	4	4	3	3	3	2	2	2	1	1	1
5. Total Leaf Area	PROV:	L	M	L	M	L	M	T	T	M	L	T	T
	TMT:	2	2	1	3	3	1	1	2	4	4	3	4
6. Total Leaf Number	PROV:	L	M	M	L	L	M	T	T	M	T	L	T
	TMT:	2	1	2	1	3	3	1	2	4	3	4	4
7. Leaf Length	PROV:	L	L	M	L	M	T	L	M	T	M	T	T
	TMT:	2	1	2	3	3	2	4	1	1	4	3	4
8. Number of Branches	PROV:	L	M	L	M	L	M	T	M	T	T	T	L
	TMT:	2	1	1	2	3	3	1	4	2	3	4	4
9. Branch Length	PROV:	L	M	L	M	M	L	T	M	T	T	L	T
	TMT:	2	1	1	2	3	3	1	4	2	3	4	4
10. Shoot:Root Ratio	PROV:	L	M	M	M	L	M	T	L	L	T	T	T
	TMT:	3	4	1	3	2	2	3	4	1	1	2	4

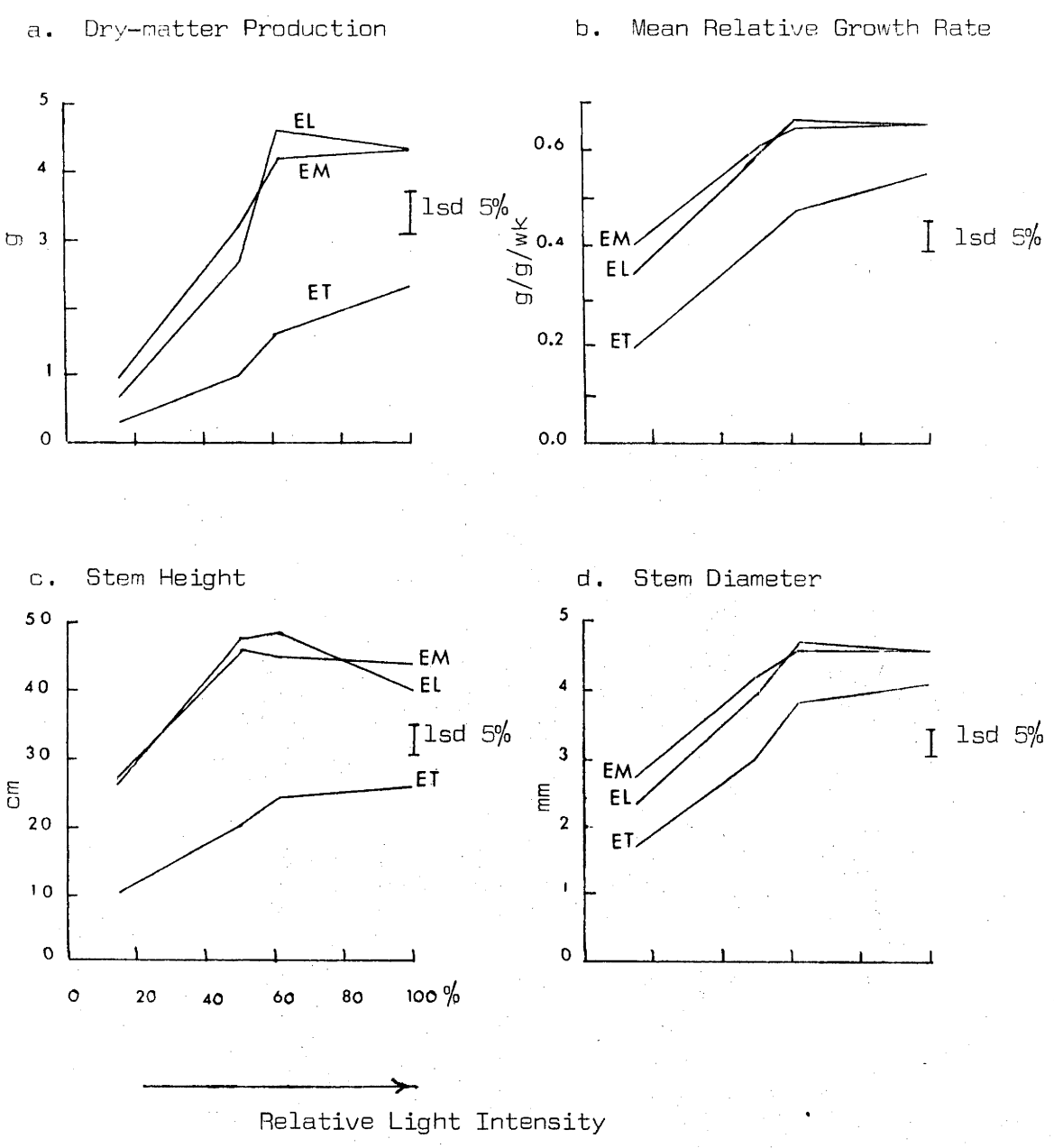
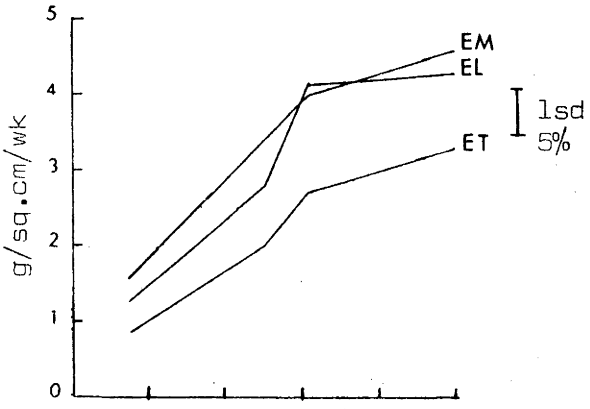
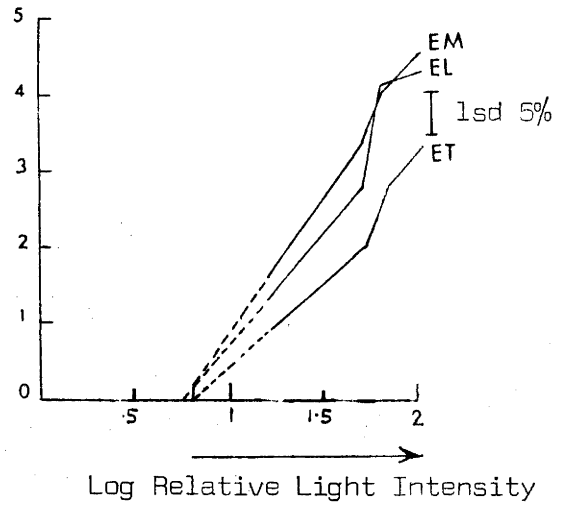


FIGURE 13.2 Growth Response of Seedlings of *Eucalyptus decaisneana* to Different Levels of Light Intensity. Seedlings Grown from Low (EL), Middle (EM) and High (ET) Altitude Sources.

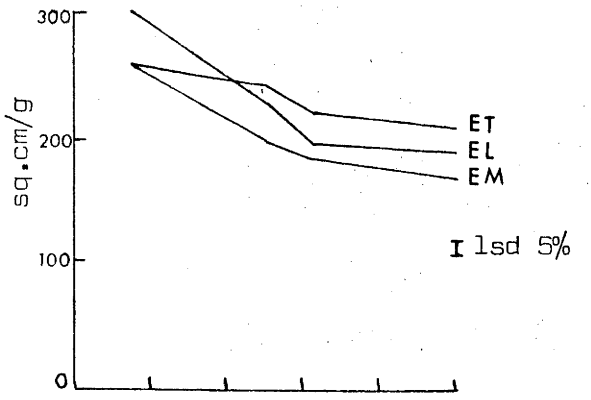
e. Mean Net Assimilation Rate



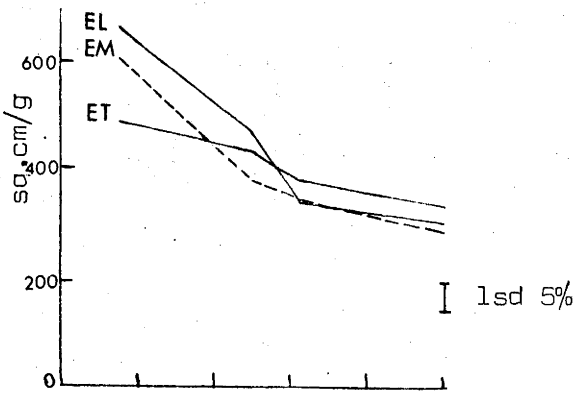
f. Mean Net Assimilation Rate



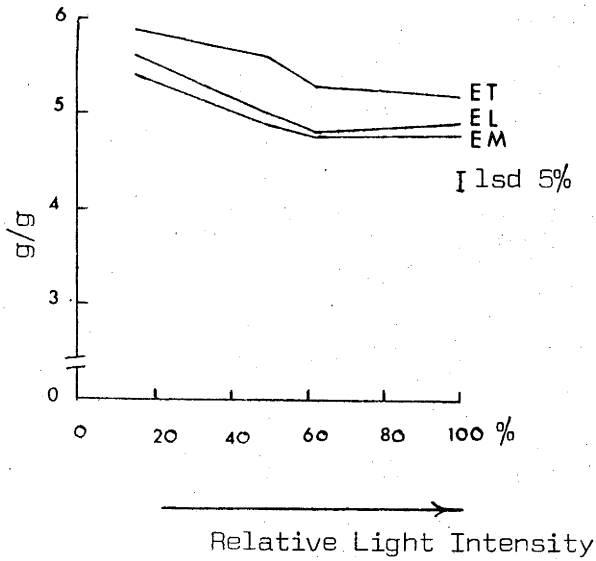
g. Leaf Area Ratio



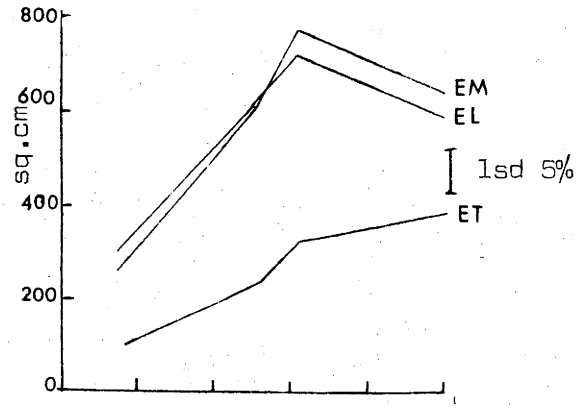
h. Specific Leaf Area



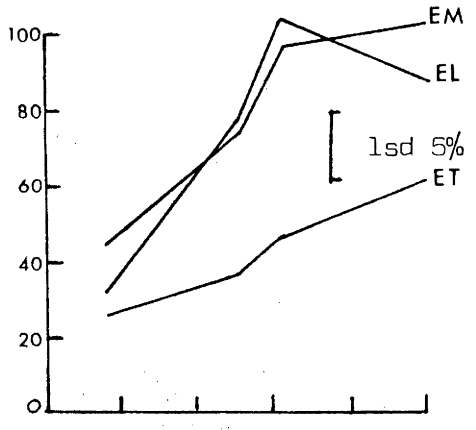
i. Leaf Weight Ratio



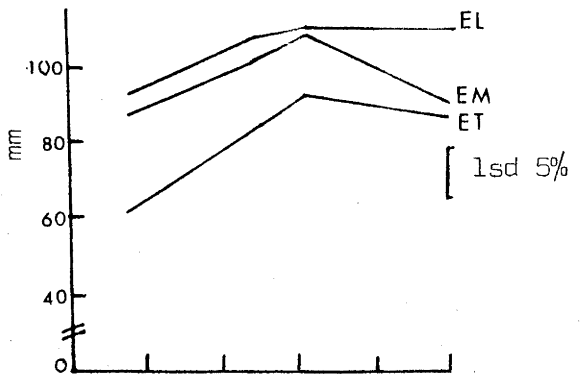
j. Leaf Area



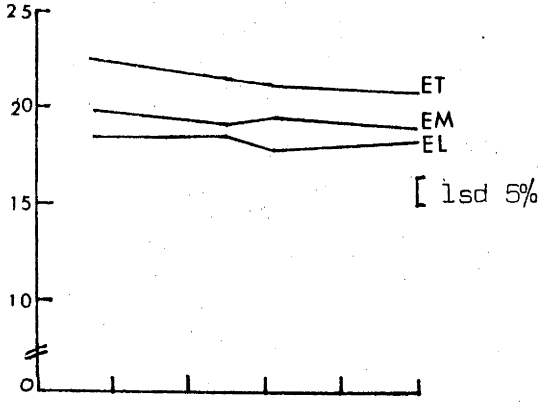
k. Total Leaf Number



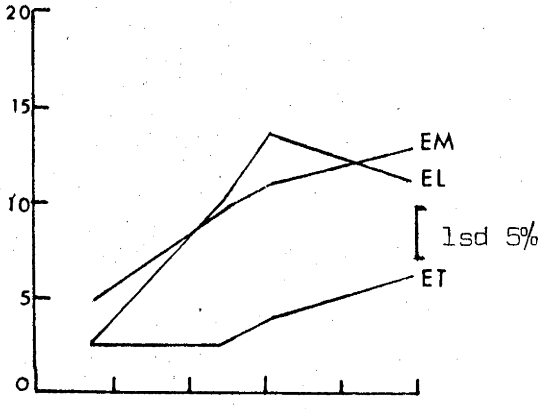
l. Leaf Length



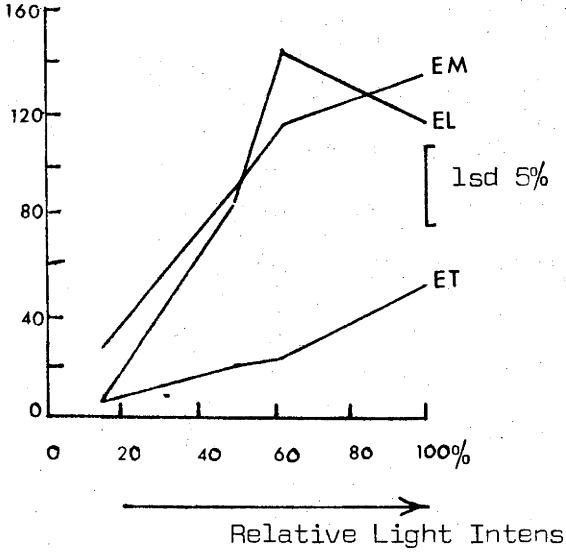
m. Leaf Length/Breadth



n. Total Branch Number



o. Total Branch Length



p. Shoot:Root Ratio

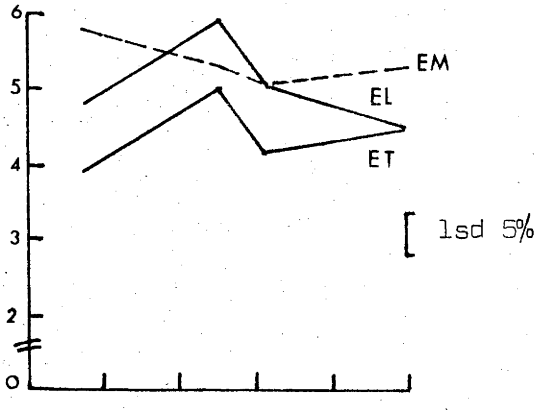


Figure 13.2.c. The average daily radiation levels at CERES phytotron during the months of treatment (November - December) were approximately 630 - 640 g.cal/sq cm/day.

ET provenance had generally significantly lower growth rate values than those of the lower provenances (EL and EM), Figures 13.2a-d. An exception was dry-matter production under heaviest shade where ET was not significantly lower than EL.

Generally, growth in ET decreased slightly under low shade (62% - 100%) but not significantly except for dry-matter production (Figure 13.2a). Growth reduction with further shade (<62%) was significant. The response curves for dry-matter production in ET was approximately linear in contrast to those of the lower provenances (EL and EM). Notably also, the optimum light intensity for growth in ET was probably greater than the full light intensity received during treatment.

13.3.2 Analysis of Productivity

Photosynthetic efficiency (indicated by NAR) generally declined with increased shade intensity, and was highest under full light (Figure 13.2e). There were slight differences between the lower provenances (EL and EM) with EM slightly more efficient than EL except at 62% light. ET in contrast, was significantly least efficient than the other provenances except under heaviest shade.

Leaf area ratio (LAR) increased with shade, being highest under heaviest shade and lowest under full light (Figure 13.2g). The response pattern in ET differs from those of the lower provenances

(EL and EM). The increase in LAR with shade in ET, was approximately linear whilst EL and EM exhibited a sharp increase in LAR with increasing shade below middle intensities (51% - 62%). Interestingly, EL was not significantly affected by low shade (62% - 100%)

The lower growth rate in the top provenance (ET) compared with the other provenances was due to the low NAR in this provenance. The effect of a generally significantly higher LAR relative to EL and EM was offset by the lower NAR value (Figure 13.2e,g).

It is possible to estimate the light compensation point (light intensity where net photosynthesis is zero) by projection of NAR values (cf. Loach, 1969). Projection of NAR values on to the axis for light intensity (in log values) gives a value for the light compensations points (Figure 13.2.f). The provenance values estimated were between 0.75 - 0.80 (inclusive) or corresponding with 5.6% - 6.3% light intensity. The difference in light compensations points between E. decaisneana provenances can thus be considered small.

13.3.3 Analysis of the Photosynthetic System

Both specific leaf area (SLA) and leaf weight ratio (LWR) were generally unaffected by low shade but increased significantly under heavy shade (Figure 13.2h, i). The response patterns in ET were approximately linear with a relatively low gradient. In contrast, the upward inflexions for EM and EL noted in LAR curves at middle light intensities were also evident in both the SLA and LWR response curves.

LWR values in ET were generally significantly higher than those in the lower provenances (Figures 13.2i) whilst EL and EM had values which did not differ significantly.

There were no significant differences in SLA between provenances under low shade (Figure 13.2h), but under heavy shade (62%) ET was significantly smallest.

Thus, under low shade (62%-100%), both SLA and LWR were important in determining size of the photosynthetic system (indicated by LAR) as apparent in the similarity of their altitudinal trends with those of LAR (Figures 13.2g, h, i). Under heavy shade (15% - 51%) differences in LAR between the lower provenances (EL and EM) were due to differences in both SLA and LWR - both parameters being greater in EL than in EM (Figures 13.2.h, i).

The low LAR value in ET relative to that of EL under the heaviest shade was primarily due to low SLA which offset the effect of a higher LWR. The high LAR value in ET relative to EM at 62% light was due to its greater SLA and LWR values.

13.3.4 Leaf and Branch Parameters

(a) Leaf Parameters

Total leaf area of the lower provenances (EL and EM) did not differ significantly but that for ET was always lower (Figure 13.2j). There was marked change in leaf area with shade. EL and EM exhibited greatest leaf area at medium shade (61%) but leaf area of ET declined steadily with increasing shade.

The similarity of leaf area in EL and EM was reflected in a general similarity in both leaf number and leaf shape (length and length/breadth). ET always had fewer leaves than the other provenances and the leaves tended to be shorter and narrower:

There was a tendency in all provenances to produce fewer and shorter leaves in heavy shade but leaf shape (length/breadth) did not change with shade intensity.

(b) Branch Parameters

In the two lower provenances (EL and EM) branch number and length was significantly reduced under heavy shade. The top (ET) provenance always had fewer and shorter branches than the others and the decline in these parameters with shade was not so marked although present.

13.3.5 Shoot:Root Ratio

There were differing patterns of provenance response to shade in shoot:root ratio. EM showed little change in shoot:root ratio except for a tendency for an increase with increasing shade. EL and ET showed no significant change in shoot:root ratio with shade except for significantly higher value at the 51% level. ET generally had lower shoot:root ratio than the other provenances.

13.4 DISCUSSION

13.4.1 Shade Tolerance of E. decaisneana

The shade tolerance of E. decaisneana is unknown. Its successional status however suggests it is a shade intolerant species

as is general for pioneer species dominating secondary forest stands in the tropics (Richards, 1964). This suggestion is however necessarily tentative in view of the absence of valid standards for comparison among tropical species.

E. decaisneana appears to be less intolerant of low shade than of high shade. This is apparent from the differences in response patterns of NAR and LAR (Figures 13.2e, g). The change in these parameters under low shade (100%–62% of full light) was generally less than the change under high shade intensities (51%–15%). The net effect is thus in the maintenance of a high growth rate under low shade above 62% light (Figure 13.2b).

Provenance differences in the tolerance of low shade intensities apparently occur in E. decaisneana. It is clear from Figures 13.2e, g, that the NAR and LAR of the low provenance (EL) were little affected by low shade in contrast to the NAR and LAR values of the upper provenances (EM and ET). It can thus be considered that the high RGR in EL under low shade was mainly due to its shade tolerance. In comparison, EM and ET were both intolerant of low shade due mainly to the reduction in their photosynthetic efficiency (as indicated by NAR). High RGR in EM and ET was however maintained by the significant increase of the photosynthetic system (as indicated by LAR) which is characteristic of shade intolerance (e.g. Loach, 1970).

It is difficult to determine whether real differences in shade tolerance occur in E. decaisneana in response to high shade intensities (62%–15%). The reduction in photosynthetic efficiency between provenances was approximately similar (60%–68%) and there

was also little difference in their projected light compensation points (5.6% - 6.3%, Figure 13.2f). Whether differences to high shade intolerance occur in E. decaisneana is difficult to ascertain from these data. Further investigation is necessary.

It is interesting to note that relative provenance differences in RGR and DMP were generally not significantly affected by shade despite differences in tolerance to low shade intensities. Notably, the RGR and DMP of the lower provenances (EL and EM) were similar whereas the top provenance (ET) had lower values irrespective of shade intensities. Thus, despite shade variation, provenance differences in productivity observed under full light at 27/22^{o}C are generally retained.

The conservation of altitudinal trend under shade was further exhibited in other parameters. For example, the lower provenances (EL and EM) were generally similar in NAR, leaf weight ratio, stem height and diameter, leaf area, leaf number and shape, branch number and length. In contrast, the top provenance (ET) always had lower values except for leaf weight ratio and leaf shape (leaf length: Breadth) which were always higher. In addition, provenance differences in LAR was also maintained under shade except under the heaviest shade (16%). Hence, it can be suggested that, variation in E. decaisneana due to altitude is stronger in expression than variation due to shading at the 27/22^{o}C temperature regime.

13.4.2 Practical Application of Results of Experiment

Manipulation of the stand light climate is a standard silvicultural tool in the regulation of stand structure and composition in natural stands. For this reason it is important to determine variations in tolerance between species or provenances.

It is difficult to extrapolate results of controlled experiments to the field. In this experiment for example, the possibility of a light intensity x temperature interaction occurring should be considered. Accordingly, ectrapolation of the results is essentially limited.

It is clear from the results that the altitudinal trend in productivity was not affected by shading despite provenance variation in shade tolerance. The top provenance (ET) can thus generally be excluded as a seed source due to its consistently low productivity unless field conditions indicate otherwise.

Both EL and EM might be equally suitable for enrichment plantings in view of the similarity in their productivity irrespective of shading. In the promotion of these provenances in the natural stand, especially in the release of seedlings, light intensity should not be allowed to fall too low.

In open plantations with EL and EM the problem of shading by weed species could be important especially during the establishment stage and might be crucial on good sites where growth of weed species may be abundant. The shading of E. decaisneana seedlings by weed species may well constitute a major problem in its large scale plantation. Poorer sites may be preferred for E. decaisneana where weed species may not thrive as well as on good sites. Indeed, in its natural habitat the species is adapted to fire degraded sites where the chances of its survival is greater with reduced competition from other secondary forest species.

PART VI

DISCUSSION

CHAPTER 14

DISCUSSION

The main objectives of the present study were -

1. to determine the major environmental factors affecting the growth of tropical highland species;
2. to determine whether intrspecies differences occur within highland species with wide altitudinal ranges.

These are discussed in the light of findings as outlined in Part V. Finally, application of growth analysis studies to forestry in the tropical highlands is outlined.

14.1 FACTORS AFFECTING GROWTH OF TROPICAL HIGHLAND SPECIES

The major factors examined, namely temperature, light and frost, significantly affect growth of the highland species and provenances studied. Expectedly, response was most marked under limiting conditions as found under low temperature and low light intensity. Where conditions were generally favourable to growth, as in the higher temperature range of the Oocarpa and Eucalyptus series ($24/18^{o}$ - $30/24^{o}$C), variation in growth response was negligible. These broad observations are however qualified by variations in response between parameters and growth factors.

Response pattern may vary widely between parameters. The temperature experiments with the Eucalyptus and Oocarpa series provide a good example since growth response can be compared between

two sets of conditions, 1. favourable (High temperature range) and 2. limiting (low temperature range). Despite species differences between the two experiments, parameters can be commonly categorised according to their response pattern. Thus, shoot:root ratio, specific leaf area (eucalypt only) and in particular, net assimilation rate (NAR) and stem height were most sensitive to temperature variations, irrespective of growth conditions. Dry-matter production (DMP), relative growth rate (RGR), leaf area and leaf area ratio (LAR) - the latter two in eucalypt only - were sensitive only under limiting conditions whereas leaf weight ratio was totally unaffected. Species difference was however apparent in the latter case since in the Kesiya series variation in leaf weight ratio with temperature was not significant.

Most of the productivity-oriented parameters, in particular DMP and RGR, fall in the second category, i.e. they are responsive to factor variation only under limiting conditions hence, they have a broad response range. For example, dry-matter production in the Oocarpa series and RGR in the Eucalyptus series were only significantly depressed under treatments with night temperature as low as $15^{o}C$. Similar observations were made in DMP of the Kesiya series. However, NAR in the latter series vary significantly between provenances. Tolerance of a wide treatment range is a desirable trait for it implies growth potential over a wide range of altitude.

It is also apparent from the study that E. decaisneana responded differentially to different environmental factors. The species seemed more intolerant to limiting light intensity than to

limiting temperature. Thus, whilst DMP was tolerant over a wide range of temperature, as noted above, it proved intolerant to even the middle shading treatment (< 62% relative light intensity). In the top provenance DMP was reduced under even lighter shade (< 100%).

In the temperature experiments as noted above RGR differed significantly with varying temperatures. The relative importance of NAR and LAR in determining growth rate appear to differ between Eucalyptus and Pinus species. In E. decaisneana leaf area ratio was relatively more important. This was specifically more due to greater specific leaf area than to leaf weight ratio. In comparison, in both Oocarpa and Kesiya series, photosynthetic efficiency was relatively more important in determining relative growth rate.

In general, the climatic factors tested significantly influenced growth of the highland species. More importantly, intraspecies variations in growth response to the variations of these factors were clearly shown. The results thus generally agree with the suggestion that climatic factors are primarily important in growth and differentiation of tropical vegetation (Section 3.6).

14.2 INTRASPECIFIC DIFFERENCES IN HIGHLAND SPECIES

The most important finding of the study is the existence of genetic differentiation in tropical highland species in both Eucalyptus and Pinus species. The choice of the study materials enable comparison between two types of distribution patterns, 1. the continuous and 2. the discontinuous or disjunct distribution. Intraspecies variation within each pattern is discussed. Genecological adaptation

within each type and its implication on provenance distribution are examined, followed by discussion on a possible evolutionary process in tropical highland species.

a. Continuous Distribution Pattern

Within the continuous distribution pattern are included E. decaisneana and the Zambales and Cordillera provenances of P. kesiya. The most important characteristic of the distribution pattern is the clinal variation in its parameters with altitude; mainly the general decrease in magnitude of plant parameters with elevations. The most important physiological trend is the decrease in productivity with elevation; specifically the reduction in DMP and RGR. Among the Pinus species, the reduction in growth with elevations was mainly due to the reduction in photosynthetic efficiency. However, among cordillera provenances of P. kesiya, the photosynthetic apparatus appeared equally important. This observation seems to contradict trends reported for temperate conifers. For example, Sweet and Wareing (1968) and others, generally found small or lack of differences in photosynthetic efficiency between provenances. Further, among temperate conifers, photosynthetic efficiency generally increased with elevation (e.g. Wright, 1971).

Variation in frost resistance in E. decaisneana however showed no altitudinal cline. Studies on temperate highland Eucalyptus species (e.g. Paton, 1972) recorded similar results. An altitudinal pattern was however apparent above a certain critical altitude but more intense altitudinal sampling in E. decaisneana is necessary to verify this.

Clinal variations in morphological characters were apparent, and generally more marked than physiological characters. These include the reduction with altitude in dimensional features such as height, diameter, leaf size and branch length and in numerical features as leaf and branch number.

b. Discontinuous Distribution Pattern

The discontinuous or disjunct distribution pattern include the Kesiya series.

In the Kesiya series, comparisons between the southern top provenance (ST) of the Zambales region with the northern Cordillera provenances (NT, NM, NL) generally showed no significant variation. ST is latitudinally disjunct from the Cordillera provenances but of comparable altitude taking into consideration the Mountain Mass Elevation Effect (see Section 2.2.1). It appears that at comparable elevations the geographic isolation between ST and the Cordillera provenances did not produce any significant raciation.

It may thus be suggested from these findings that environmental differences due to altitude exert a much stronger selection force than that due to geographic isolation.

c. Genecological Adaptation

In discussing adaptation within altitudinal species, it is instructive to define the ecological framework within which the environmental factors studied operate. The species used in the study are basically pioneer species which are maintained in fire-subclimax formations (Luckhoff, 1964; Turnbull, 1971, pers. comm.). They are therefore essentially limited in their distribution by biotic factors,

notably competition from surrounding primary climax vegetation which were initially displaced by fire. It is within this framework that local environmental factors exert their differentiating effects on the species.

Genetic differences attributed to temperature, light and frost have been discussed in the various experiments. The important thing to note is that these differences appear localised to specific altitudinal zones as evident from the altitudinal pattern observed in the numerous interactions between provenance and environmental factors studied. Further, their genetic pattern of altitudinal differences is very strong in many parameters studied. For example, the greater productivity and growth rate in the low provenance of the Eucalyptus series is maintained throughout the range of temperature and light intensity applied. The differential characters within the species are thus probably a result of genecological adaptation to local selection pressures.

This suggestion can be further augmented. In species with the continuous distribution, genetic differentiation must be due to strong selection pressures since genetic continuity will tend to be maintained even though the rate of gene flow may be slow. In addition, these pioneer species are characteristically heterogeneous, prone to panmixis and genetic flexibility (Rehfeld and Lester, 1968) i.e. their propensity is towards maintaining the integrity of the gene pool. Thus the pressures strong enough to reverse this trend will have to be directional and hence adaptational in nature.

d. Possible Speciation Process in Tropical Highland Environment

In tropical lowlands vegetation, speciation is heavily influenced by genetic drift (Federov, 1966) and selection pressures due primarily to the botanical component of the environment (Dobzhansky, 1950). These suggestions were based on the assumption of the existence of a relatively uniform physical environment.

It is clear from the review in Chapter 3 that the tropical highland ecosystem is diverse in terms of both botanical and physical components. The speciation process may not necessarily resemble that in the lowland environment. Further, the study showed evidence that species with a wide altitudinal range displayed significant intraspecies differences in growth response to the physical factors tested - temperature, light and frost. Such a response is clearly adaptational and it can thus be suggested that the speciation process in tropical highland species, must definately incorporate a response to the physical environment.

14.3 APPLICATION OF GROWTH ANALYSIS STUDY

14.3.1 Species and Provenance Selection

The study amply proves the existence of genetic differences in important economic features such as productivity and growth rate, in tropical highland tree species. The species studied are timber species with succesional status probably similar to most other highland species that are popular in plantation programmes in the tropics (e.g. *Pinus merkusii*, *P. insularis*, *P. patula*, *P. occidentalis* etc). Numerous field trials have established provenance differences that

are mainly geographic in nature. It is evident from the study that geographic differences may be smaller than altitudinal differences despite the deceptively close proximity of seed sources within an altitudinal population. For this reason, seed collection in the highlands should include samplings from different altitudes.

In view of the above consideration, the importance of assessing genetic variability within highland species for the purpose of mapping out seed collection zone should be emphasised. For this purpose growth analysis method is suitable in view of its speed in assessing differences in growth and productivity.

Another important application of the method is in tree improvement. The method can separate and relatively assess the components of growth rate (assimilation rate and leaf area ratio). The more important component may then be selectively bred to improve growth rate and productivity. The feature can also be combined with other desired characters.

14.3.2 Determination of Species or Provenance Potential Range for Optimum Growth

The objective of a species or a provenance trial is to match the species/provenance to a given site for the optimum production of a desired plant character - usually wood - within allowable constraints. The trials mostly concern the introduction of exotics but may also include indigenous species.

Growth analysis method can assist in the selection of seed source and in the location of trial sites. As illustrated in the

study, important environmental factors can be determined and the potential optimum range mapped out for the location of trial sites.

Caution in the field projection of growth analysis results has been emphasised. Error may be minimised if adequate field work is conducted in measuring environmental factors at source and the major factors and their combinations sufficiently covered. Since field trials may take years to conclude the investment in these studies are thus worthwhile.

Some Malaysian examples will serve as illustrations. Trials with P. caribaea var. hondurensis, the most promising exotic, have shown generally good growth up to 600m elevation (Freezaillah, 1966). At 1500m growth was considerably reduced. Experiment on the same variety (Chapter 10) suggests optimum growth temperatures at 24/18^{o} to 27/18^{o}C with dry-matter production significantly reduced at night temperatures cooler than 15^{o}C, the altitudinal equivalent of night temperatures at approximately 900m. The cardinal temperatures from the experiment may thus be used as guides to the location of trial plots.

Another area of potential application is in autecological studies on seedling establishment and distribution of important species in the Highland Dipterocarp Subzones. An outstanding problem presently facing Malaysian forestry is to ensure adequate regeneration of favoured species in these forests (Section 2.3.1). Growth analysis studies can be conducted on seedlings of these species to determine their growth requirements for successful establishment.

A related problem is that of species distribution. Knowledge of factors determining natural limits of distribution is important if the extension of these species is desired. It is apparent from the present study that good growth can still be maintained outside the range of an environmental factor, say temperature, normally experienced in its natural distribution. This possibility has been demonstrated in a field experiment wherein seedlings of Shorea platyclados continued to thrive when transplanted well below their lower natural limit (Lall Gill, 1969). Such experiments can be complemented with growth analysis studies covering the range of environmental factors considered important to establishment.

APPENDIX I

CLASSIFICATION OF FOREST VEGETATION OF PENINSULAR MALAYSIA

1. After Symington (1943)

I.	Climatic Climax Formations	(1) Lowland dipterocarp forests	(a) Malayan type (b) Burmese type
		(2) Hill dipterocarp forests	(a) Inland type (b) Coastal type
		(3) Upper dipterocarp forests	
		(4) Montane oak forests	
		(5) Montane ericaceous forests	
II.	Edaphic Climax Formations	(6) Mangrove swamp forests	
		(7) Beach forests	
		(8) Peat swamp forests	
		(9) Riparian fringes	(a) Brackish type (b) Freshwater tidal type (Rassau rivers of Corner). (c) Gallery forests (Nera rivers of Corner) (d) Saraca streams (this is Corner's name)
		(10) Other swamp forests	(a) Basong (Alstonia spathulata) swamps (b) Malabira (Fagraea crenulata) swamps (c) Bungor (Lagerstroemia) swamps (d) 'Lopak' (seasonal swamps)
		(11) Heath forests	
		(12) Limestone forests	
III.	Biotic Climax Formations	(13) Schima-bamboo forests	
		(14) Gelam (Malaleuca leucadendron) swamp forests	
IV.	Unstable Forests or Forests of Uncertain Ecological Status.	(15) Coastal padang formation	
		(16) Adinandra forests	
		(17) Regnerated forest	

APPENDIX I (Cont'd)

2. After Wyatt-Smith (1963)

Lowland evergreen rain forests

1. Lowland Dipterocarp Forests
2. White Meranti-Gerutu (Seasonal) Forests
3. 'Heath' Forests
4. Hill Dipterocarp Forests
5. Upper Dipterocarp Forests

Lower montane forests

6. Montane Oak Forests

Upper montane forests

7. Montane Ericaceous Forests

Swamp and low-lying forests

8. Marine Alluvial (Mangrove) Swamp Forests
9. Peat Swamp Forests
10. Freshwater Alluvial Swamp Forests
11. Riparian Fringes

Miscellaneous forests on sites with severe drainage and on those deficient in available moisture due to violent winds or to low temperature

12. Beach (Strand) Forest
13. Limestone Vegetation
14. Vegetation of Quartz Dykes, Quartzite Ridges and other sterile habitats with severe drainage or lacking available moisture

Regenerated forests

15. Regenerated Forests

APPENDIX II

FOREST TYPES ASSOCIATED WITH THE HIGHLAND DIPTEROCARP SUBZONES

Forests of the Highland Dipterocarp Subzones are economically the most important natural vegetation of the Malaysian Highlands. The various recognised forest types that make up the Highland Dipterocarp Subzones are shown in Figure 2.1. The economically important forests are mainly found in the Hill Dipterocarp Subzone. These are briefly described below.

(a) Seraya Ridge Forests (Shorea curtisii)

The forests, considered among the most productive in the country, are found throughout the Main Range. The principal species, Shorea curtisii, is the commonest and most important timber species in the Hill Dipterocarp Forest.

The species occur semi-gregariously along with other subsidiary species on ridges. Gradient is influential in determining its altitudinal limits.

Common subsidiary species include Anisoptera curtisii, Artocarpus lanceifolius, Calophyllum inophylloide, Hopea beccariana, Hopea spp., Myristica gigantea, Tarrietia javanica, Swintonia spp., and Vatica spp. On coastal areas there are slight changes in subsidiary species but the flora is essentially the same. Mixture with Balau kumis-damar hitam forests is however, frequent.

Density of middle sized trees and of saplings is poor. Ground flora is often absent due to heavy shading from Bertam (Eugeissona triste). Refer Section 2.1.

(b) Balau Kumis-damar hitam Forests (Shorea laevis - Shorea multiflora)

The principal timber species are Shorea laevis and Shorea multiflora. The former is the second most important economic species in the hill forests.

The forest type is often associated with Seraya Forests on ridges and occur widely throughout the Main Range, particularly in Selangor, Negri Sembilan and in Pahang. Unlike Seraya, however, their distribution commonly extends down to the upper slopes.

(c) Balau laut Forests (Shorea glauca)

The principal species is Shorea glauca occurring frequently in association with Shorea maxwelliana and Sindora wallichii.

The forest type is normally found on coastal hills from sea level to a few hundred metres in altitude rising to higher elevations in inland forests. It is common on the lower and often steeper slopes and is gregarious on seaward aspects.

(d) Balau-keruing Forests (Shorea spp. - Dipterocarpus spp.)

The principal species and their regional occurrence are Shorea atrimervosa (east coast), Shorea foxworthyi (east coast and Perak), Dipterocarpus costulatus, Dipterocarpus appendiculatus (east coast), Dipterocarpus fagineus, Dipterocarpus penangianus, Dipterocarpus pseudofagineus found in all states. Subsidiary species of Red Meranti timber grade are also found.

The forests are particularly common along the east coast of Johore, Pahang and Trengganu. They are also found on the western slopes of the Main Range in South Kedah and Perak.

(e) Merpauh Forests (Swintonia spicifera)

Swintonia spicifera, the principal species, forms almost pure consociations on ridges at elevations higher than the Seraya ridge forests. Its upper limits often overlap with the Upper Dipterocarp forests.

(f) Keruing-resak-mengkulang Forests (Dipterocarpus spp. - Vatica cuspidata - Tarrietia simplicifolia)

The forest type has several species: Dipterocarpus costulatus, Dipterocarpus sublamellatus, Shorea acuminata, Tarrietia simplicifolia and Vatica cuspidata. The latter is the most characteristic species. Subsidiary species include Koompassia malaccensis, Shorea spp. (balau).

APPENDIX III

Vegetation Structure and Physiognomy in the Lowlands and Montane Zones.

	LRF	LMRF	UMRF	Authority
No. tree stories	3	2	1	2
Density:				
Woody indiv. > 2m/0.25 ha.	353	539	610	2
Indiv. < 1m/100sq.m.				
Tree seedlings	151	94	nr	2
Shrubs	1	0	nr	2
Herbs	66	1325	nr	2
Vines	209	146	nr	2
Total	427	1565	nr	2
Indiv. > 1' girth/100ac.	1600	1100	-	1
..... > 6'	800	100	-	1
..... > 10'.....	80	-	-	1
Trees ≥ 4" dbh/10,000sq.ft.	55	46	nr	3
..... ≥ 8" dbh/.....	27	28	nr	3
Individuals/454 sq.m.				
'seedling layer' (0-3').	1387	1214	nr	3
'sapling layer' (3-9').	88	190	nr	3
'pole layer' (9-20').	93	70	nr	3
Total	1568	1474	nr	3
Woody indiv. > 2m/0.25ha.				
1st storey trees	16	52	405	2
2nd storey trees	54	487	-	2
3rd storey erect woody plants	283	-	-	2
Diameter:				
1st storey trees. Greatest D. cm.	96	85	-	2
..... Av. Diam. cm.	53	34	-	2
2nd storey	28	18	-	2
3rd	16	-	-	1
Av. tree girth ft.	7-8	4-5	-	3
Av. diam. (≥ 8" dbh) ins.	13	12	nr	
Volume:				
1st storey trees. cu.m.	49	33	-	2
2nd	25	8	-	2
3rd	2	-	-	2
Total	76	41	-	2
Height:				
Tallest trees. m.	36	22	13	2
1st tree storey. Av. hgt. m.	27	17	6	2
2nd	16	4	-	2
3rd	10	-	-	2
Canopy hgt. ft.	70-100	60	15-25	1
Trees 8" dbh. av. hgt. ft.	81	71	nr	3
Av. hgt. m.	nr	nr	15	4

APPENDIX III (Cont'd)

	LRF	LMRF	UMRF	Authority
Leaves:				
Size. No. indiv. >1m/0.25ha.				
microphylls	7	15	285	2
mesophylls	295	530	280	2
macrophylls	38	18	-	2
Lengths.				
% indiv. <10cm.	9	7	70	2
% ..... >10cm.	19	4	0	2
Shape				
compound. % indiv.	22	11	0	2
>1m. height.				
entire margin. % indiv.	80	75	78	2

Authority: 1. Beard 1946
2. Brown 1919
3. Grubb et.al. 1963
4. Richards 1936

LRF Lowland Rain Forest
LMRF Lower Montane Rain Forest
UMRF Upper Montane Rain Forest

APPENDIX IV

NOTES ON SEED SOURCES USED IN EXPERIMENTAL WORK

A. EUCALYPTUS DECAISNEANA

Distribution: E. decaisneana is a tropical species native to the island or Timor; 8°-11°S, 123-121°E. It is one of the few Eucalyptus species occurring outside Australia. In Indonesian Timor E. decaisneana forests are found on the slopes of the Mutis, Molo and Miumato mountains, on the Fatu Timau in Amtoan and the Lakaan in Lamarknen. It is generally found at elevations from 1000m to 2200m. In Portuguese Timor it occurs principally in the Ramelan mountains, on Mundo Perdido and the Mata Bia Range, at elevations from 500m to 2680m (Turnbull, pers.comm.).

Climate: Monsoonal; Koppen's classification, Awi. Selected meteorological data recorded at stations nearest collection sites are given in Table IVa.

TABLE IVa Selected Meteorological Data at Maubisse[a] and Hato Buillico[b] in Portuguese Timor

	Maubisse (1432m)	Hato Buillico (1860m)
Av. daily max. temp., warmest month (°C)	30.0°	20.7°
Av. daily min. temp., coldest month (°C)	11.9°	8.6°
Frost occurrance	Nil	Occasional
Lowest recorded temp.	5.5°	-3.0°
Annual precipitation (mm)	1438	1947
Annual evaporation	1034	789

Monthly precipitation (mm)

	J	F	M	A	M	J	J	A	S	O	N	D
	DRY SEASON											
Maubisse	186	233	167	184	115	65	36	18	20	29	137	245
Hato Buillico	356	384	249	212	150	77	22	18	10	25	135	309

(a) Lat.8°50'S Long.125°36'E
(b) Lat.8°54'S Long.125°31'E

APPENDIX IV (Cont'd)

Fog occurs throughout the year in the north coastal range south of Dili, between 500m - 1300m altitude. In the Central mountain regions fog frequency is reduced except at higher elevations.

Forest Types and Habitat

Between 500m to 1200m, stands are best developed on mesic sites as in gullies and poorest on xeric sites, as on exposed ridges, where E. decaisneana is often displaced by more hardy species such as E. alba. Fog influence is important in creating mesic conditions.

Above 1500m the environment is more montane and mesic and fog is less important in stand development and distribution. Above 2200m stands are more open and trees smaller with poorer form than those at lower elevations.

B. PINUS KESIYA ROYLE EX GORDON

Species distribution in the Philippines: Refer map in Figure IVa. The species "occurs in the Philippines on the island of Luzon between latitudes $15^{o}30'$N and $18^{o}15'$N at altitudes from 450m to 2450m. The principal occurrance is in the Central Cordillera mountain range in Northern Luzon but smaller stands are found in the Caraballo and Zambales mountains", (Turnbull, 1971).

Climate: Monsoonal, with a dry season from five to seven months. Annual fluctuation in rainfall is the most important climatic change.

Selected meteorological data taken at Baguio City in the south of the principal distribution area (in the Central Cordillera mountains) are given in Tabel IVb.

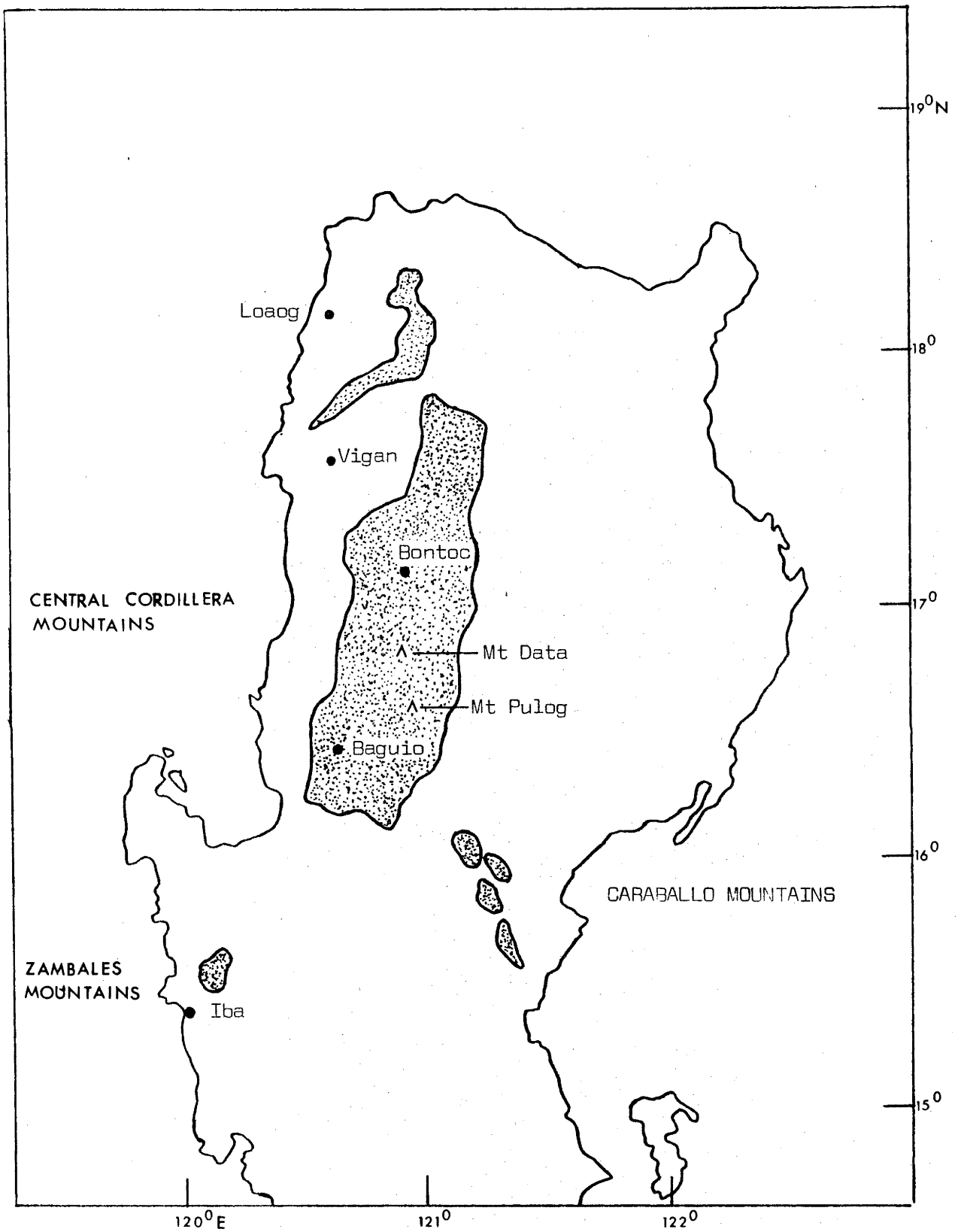


FIGURE IVa Natural Distribution of P. kesyia in Northern Luzon, The Philippines (After Turnbull, 1971)

APPENDIX IV (Cont'd)

TABLE IVb Selected Climatic Data at Baguio City, The Philippines

Altitude 1200m; Lat.7°12'N; Longt. 12°26'E

	Dry Season											
	N	D	J	F	M	A	M	J	J	A	S	O
Rainfall (mm)	122.8	49.7	23.1	20.3	46.4	116.7	391.5	429.9	1068.3	1137.6	699.7	378.9
No. of Rain Days	10	6	4	3	6	10	21	23	28	27	25	19
Mean Temp.(°C)	17.9	17.3	16.6	17.0	18.0	18.9	18.9	18.6	18.0	17.7	17.9	18.0
Mean % RH	83.1	80.5	79.9	79.7	80.0	83.0	87.7	89.7	92.3	93.5	92.0	88.5

APPENDIX IV (Cont'd)

Temperature: Average temperatures fluctuate little throughout the year.

Above 1500m the average annual temperature is about 18°C (17°C January to 19°C in May) and below 1500m about 25°C (23°C January to 28°C in May). At higher elevations maximum temperature is considerably depressed by fog.

Frost: Light frosts occur above 1500m in December and January.

Rainfall: Rainfall during the wet season (April to November) is 3000mm - 5000mmat elevations above 1200m and at c.2500m (May to October) at lower elevations.

Forest Types and Habitat: Stands in major areas of distribution are generally extensive, pure and approximately even aged. They are dense at higher elevations (> 1500m) and are best developed between 1500 - 2200m on mesic sites. Stands are more open at lower elevations where regeneration is poor or non-existant especially on the more xeric S-E and S-W slopes.

The ecotones at the upper and lower limits of distribution are sharp giving way to broad-leafed montane and lowland species respectively.

C. P. OOCARPA SCHIEDE AND P. CARIBAEA VAR. HONDURENSIS B AND G

Two of the P. oocarpa seed sources (POM and POL) originated from the interior highlands of British Honduras while the P. caribaea var hondurensis seed source (PC) originated from the east coast of Nicaragua.

APPENDIX IV (Cont'd)

Distribution: The distribution of P. oocarpa in Central America is shown in Figure IVb. .

P. oocarpa is a very variable species, and widely distributed from Sonova and Chihuahua to Central America, from 300m to 2400m altitude. The variety ochoterenai grows on the high eastern part of Mount Pine Ridge in British Honduras between 300m and 900m altitude. The species is considered the most southerly pine of the New World, Mirov (1967).

P. caribaea var hondurensis grows in the Bahamas Islands, western Cuba, Isle de Pinos, Honduras, Guatemala, Nicaragua and British Honduras, ranging in altitude from sea level to 300m, Mirov (1967). In interior Honduras and Nicaragua its ranges overlap that of P. oocarpa where the possibility of hybridization has been suggested (Critchfield and Little, 1966).

Climate: Meteorological data of Mountain Pine Ridge, in British Honduras is given in Table IVc. Meterological data for the other seed sources (POT and PC) are not available.

British Honduras: The climate varies from warm moist tropical rain forest to savannah types with dry to semi-dry winter periods. Koppen's Amw" and Aw".

In the interior highlands the climate is temperate (Koppen's Cw) with marked dry winter stretching from January to April/May. Winter temperature is c.13^{o}C and summer temperature c.29^{o}C, Luckhoff (1964).

APPENDIX IV (Cont'd)

Nicaragua: On the eastern coast climate varies from Koppen's Af in the north to Amw"i in the south in Bluefields. There is a well defined semi-dry season from February to May although protracted draught is unknown (Luckhoff, 1964).

CENTRAL AMERICA

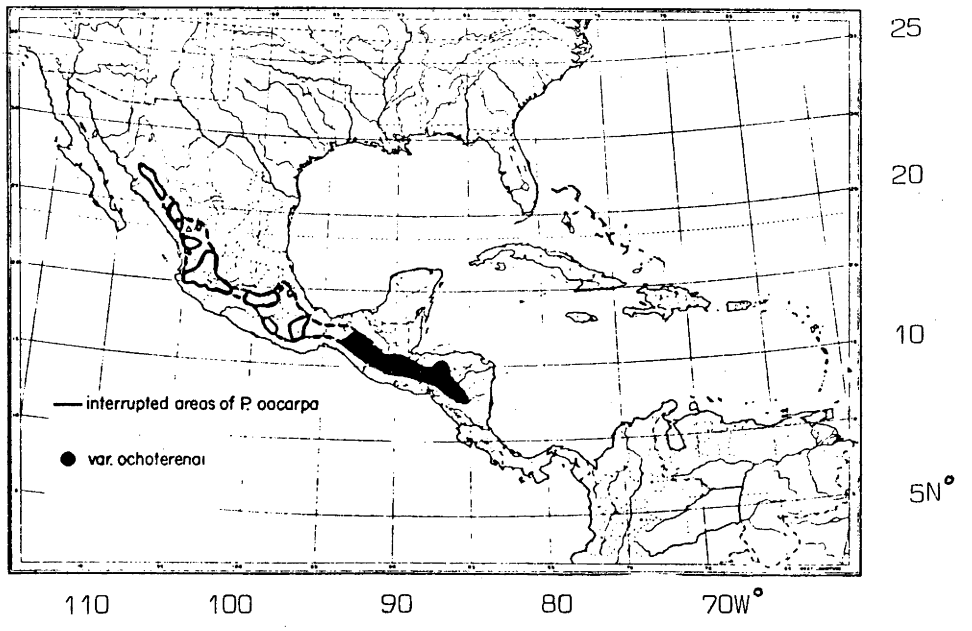


FIGURE IVb Natural Distribution of Pinus oocarpa. Darkened Area Shows the Range of Variety ochoterenai (Mirov, 1967).

TABLE IVc Meteorological Data at Cooma Cairns, Mountain Pine Ridge, British Honduras (Hudson, per.comm.)

Altitude 939m; Lat. 17°00'N; Longt. 88°51'W

	J	F	M	A	M	J	J	A	S	O	N	D
Mean Max. Monthly Temp. (°C)	21.1	22.2	24.4	27.2	28.3	26.7	25.6	26.1	26.1	24.4	21.7	21.1
Mean Min. Monthly Temp. (°C)	15.6	15.6	17.2	18.3	19.4	20.0	19.4	19.4	19.4	18.9	17.2	16.1
Mean Monthly Rainfall (mm)	171	91	78	60	70	210	233	165	253	278	325	146
Mean Monthly Rel. humidity (%) at 1500hrs.	81	75	69	64	66	74	76	75	79	81	84	83

APPENDIX V

COMPOSITION OF MODIFIED HOAGLAND SOLUTION

(Went, 1957, pp.78-79)

$Ca(NO_3)_2.4H_2O$	95 g/100 L
$(NH_4)H_2PO_4$	6 " "
KNO_3	61 " "
$MgSO_4.7H_2O$	49 " "
H_3BO_3	0.06 " "
$MnCl_2.4H_2O$	0.04 " "
$ZnSO_4.7H_2O$	0.009 " "
$CuSO_4.5H_2O$	0.005 " "
$H_2MoO_4.4H_2O$	0.002 " "
$Co(NO_3)_2.6H_2O$	0.0025 g/100 L
$FeSO_4.7H_2O$	2.49 g/100 L
EDTA	3.32 "
NaOH	0.50 "

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